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SYNOPSIS

This paper reviews the known species of Notostraca on the basis of a large collection of museum material and on information from the literature. The genus *Triops* is reduced to four, and the genus *Lepidurus* to five species.

The species of *Triops* are separated on the armature of the telson and on the presence or absence of a second maxilla; in each species there is considerable variation in the segment number, and in the many structures whose variation is shown to be correlated with this number.

The segment number is more constant in *Lepidurus* and fewer structures are correlated with its variation; this genus appears to fall into two groups, as Linder (1952) suggested, on the basis of the segment number. A new species of *Lepidurus* is described from Russia.

In addition to the analysis of the validity of the systematic characters from work on preserved specimens, evidence derived from the growth and development of living animals, their cytology, their reproduction and their protein specificity are also considered.

INTRODUCTION

THE Notostraca are an order of Euphyllopod Crustacea with shield-shaped carapace, consisting of a single family with two genera; *Triops* (= *Apus*) and *Lepidurus*. They usually occur in temporary pools of fresh or brackish water, being most common in the drier parts of the world where the surface water is often of a temporary nature.

Their adaptation to a temporary habitat has enabled their drought-resistant eggs to become efficient agents of passive dispersal, so that populations occur on remote oceanic islands and are apparently found wherever there are suitable pools.

These animals are of interest to the general zoologist not only on account of their primitive nature, but also because they exemplify an animal in evolutionary stagnation. The family has been in existence since the Permian, and forms from the Triassic are almost indistinguishable from one of the extant species.

Individually Notostraca are notoriously variable and differences in the armature of spines on the exoskeleton, or in bodily proportions, can be found in any pair of animals, even those from the same pool. This, together with the lack of conspicuous morphological discontinuities within the genera, makes the group a " difficult " one systematically, and has resulted in the excessive number of descriptions—of specimens rather than species—with which the synonymies are now burdened.

There have been several revisions of the group as a whole, but none later than that of Simon (1886) who revised the species then known to him. Barnard (1929), Linder (1952) and Tiwari (1952) have reviewed regional material from South Africa, North America and India respectively, and have tended towards a reduction in the number of species recognized, placing many names into the synonymies. This trend has been general in recent years but has by no means prevented the description of new species on inadequate grounds.

Because of their interest from a systematic and evolutionary point of view, their geological age, their passive distribution, and their restricted habitat, it was evident that a review of the Notostraca based on a comprehensive collection of preserved specimens and on a study of the growth and cytology of living animals was desirable ; one of the points of agreement between recent authors on the group has been the need for such a revision.

MATERIALS

The preserved specimens of Notostraca on which this revision is based consist of more than 200 samples, of which about 160 are of *Triops* ; the number of specimens in each sample varies and the majority contain less than 10 individuals, although a few have more than 100 specimens from the same locality.

The bulk of this material is formed by the collections of the British Museum and of the Muséum Nationale d'Histoire Naturelle, Paris ; the remainder was on loan from the U.S. National Museum in Washington, the Western Australian Museum in Perth, the Zoological Survey of India in Calcutta, and the Museo de Ciencias Naturalis in Madrid. A few samples of preserved Notostraca were sent to me by private individuals.

The living material was reared in the laboratory from eggs in dried mud sent to me from phyllopod pools all over the world. Many contained no viable eggs, but successful hatchings were obtained from the following samples (collector's name in parentheses) : *Triops cancriformis*—Sweden (P. Ardö), England (A. R. Longhurst), France (D. Schachter), Italy (H. M. Fox) ; *T. granarius*—Johannesburg (van der Horst), Grahamstown (J. Omer-Cooper), Iraq (A. James) ; *T. longicaudatus*—California (L. E. Rosenberg) ; *T. australiensis*—Ayers Rock (I. Thomas, F. McNeill, A. L. Rose), Kalgoorlie, Ballodonia (A. R. Main) ; *Lepidurus arcticus*—Iceland (H. Moore) ; *L. apus*—New Zealand (A. Lysaght, E. Percival).

Living cultures of Notostraca were successfully maintained in the laboratory

under reasonably standard conditions. Larvae hatched readily from the mud samples when these were placed in a tank of clean water (either filtered pond water or dechlorinated tap water) which were maintained at about 20° C, air being bubbled through the water. If an excess of mud was put in a tank bacterial growth was very rapid and the culture was soon lost ; about $\frac{1}{4}$ in. on the bottom of a 24 in. by 12 in. tank proved suitable.

The larvae fed at first on the organic content of the mud and if the production of diatoms and Protozoa was poor in the culture in its early stages an addition of cultured *Chlorella* was very beneficial to the growth of the larvae. From about 1 cm. in length growth was more rapid if additional food was provided ; this consisted of chopped annelid worms (*Tubifex*), live *Daphnia* and an artificial food. This last was made up from equal parts by weight of dried *Daphnia*, grass-flour, and Bemax (a proprietary cereal food) ground together into a fine powder and suspended in calcium alginate jelly. This was then chopped and formed a satisfactory basic diet for adult Notostraca.

The eggs laid in the cultures were hatched by allowing the mud which contained them to dry out slowly ; on re-wetting, a high proportion of them hatched successfully. A more rapid and effective way of maintaining a culture was to collect the eggs as they were laid and to transfer them to a beaker of clean tap water with an addition of 30–50% of glass-distilled water ; this low osmotic pressure medium induced hatching after 12–14 days without prior drying, in the same manner as Hall (1953) has described for the eggs of *Chirocephalus diaphanus*. The larvae live for only a few moments in this water however, and must be removed from it at once.

I am most grateful to those who sent me samples of mud (including those from which I was unable to hatch Notostraca and which are not listed above) and to those people who collected and sent preserved specimens. My thanks are also due to the Authorities of the Museums listed above who lent me material, and especially to the Trustees and Staff of the British Museum (Natural History) and the Muséum Nationale d'Histoire Naturelle, who generously gave me facilities for examining their collections. I am particularly indebted to Dr. J. P. Harding of the British Museum who has given me invaluable help during the whole time that I have been studying the group.

The work on living animals was done in the Zoology Department of Bedford College, University of London under the supervision of Professor H. Munro Fox, to whom I am grateful for much assistance.

A maintenance grant from the Department of Scientific and Industrial Research, and a special grant from the Central Research Fund of the University of London were received during the work.

Abbreviations.—In the text the museums listed above are referred to by the following sets of initials :

BMNH . . .	London.
USNM . . .	Washington.
MNHNP . . .	Paris.
WAM . . .	Perth.
ZSI	Calcutta.

SYSTEMATIC CHARACTERS

The systematics of the Notostraca have been based almost entirely on characters of the setae and spines which comprise the armature of the exoskeleton, and on the proportions of various parts of the body—the endites, the furca and the carapace.

The validity of these characters was discussed in Barnard's revision of the South African forms (Barnard, 1929). More recently, the review by Linder (1952) further explored this field and has added several characters which prove useful in separating species. The description of new species from European and North African material by Ghigi (1921) initiated a discussion on the validity of the characters which he used, to which Colosi (1922), Gurney (1923), and Gauthier (1933, 1934) contributed.

Before any character can properly be used in systematics it is essential that its variation in adult individuals be known, and that its development or change during the growth of a single individual should have been studied ; in the present review the validity of as many as possible of the systematic characters has been studied and several new ones are proposed.

Previous authors have been concerned almost without exception with the variation of characters in samples of adult individuals, and it has been possible to extract much useful information about this from the literature, which has been combined with that obtained from the study of the museum material.

A pure line of individuals from a hermaphrodite *Triops cancriformis* from Britain was raised under standard conditions ; a large batch of eggs was collected from the parent, hatched, and reared at first in a single large culture dish, later being transferred to individual dishes, each with the same volume of water and mud ; the dishes standing in a room thermostatically controlled at 20° C (± 1° C). A surplus of the artificial food was always available to the animals. From this culture 25 individuals were preserved and their variation studied ; all these animals were preserved after growth changes had ceased in the characters to be studied.

The change of several characters during growth was studied by Linder (1952) in museum material ; he based his conclusions on specimens which were about to ecdyse, in which both the old and the new exoskeletons could be observed. In the present review living material of all species of *Triops* was studied during growth from larva to adult ; the changes in relative proportions during growth have been examined and the size at which the exoskeletal armature becomes stable determined.

A start has also been made on the effects of environmental factors on morphology, but the experiments have not been very successful. *Triops* is a difficult animal to grow under precisely standardized conditions, for it has not been possible to rear them without a little mud in their dishes even when they are fed artificially. Main (1953) has suggested that so-called specific differences in Australian forms may be due to differences in the salinity of the medium ; I have made attempts to grow *Triops* at salinities near those that Main found in the field, but the animals have rapidly died each time. The temperature at which the animals were reared might be expected to have some effect on their form, and so a pure line of *T. cancriformis* was grown at a temperature (25–28° C) near their lethal point, but these animals showed little difference from those grown at normal temperatures.

Notostraca were grown in the laboratory under very diverse conditions of temperature, food, and vessel size, but all have remained remarkably uniform in their morphology. *Daphnia* under parallel conditions would show very marked morphological changes, and it is probably safe to assume that environmental factors can affect the morphology only after a very considerable number of generations—as salinity affects the form of *Artemia salina* only after several years (Schmankiewitsch, 1875).

The various characters which have been used in systematics are now examined separately.

(1) *Total size*

Samples of adult Notostraca usually contain individuals of very different sizes, and it is difficult to determine whether there is a normal adult size for any species. The growth rates of animals in a batch of *Triops* reared in the laboratory are also very variable (Fox, 1949) as the pure line of *T. cancriformis* showed very clearly; after a few days growth they varied enormously in size; 33 individuals were between 2·0 and 3·5 mm. carapace length, while one was only 1·5 mm., and another 5·0 mm. Spandl (1926) gives growth curves for individual *T. cancriformis*, maintaining that those which grow the fastest become the largest, which is what one would expect if the growth rate depended on the level of nutrition.

The usual adult size for all species seems to be between 15 mm. and 30 mm. in carapace length, the growth curve flattening out somewhere between these two figures.

The total size has occasionally been used as a systematic character.

Bowkiewicz (1923) suggests that giant *Triops* which he saw in Siberia might be a new species; large individuals of other species occur up to 40 mm in carapace length and probably correspond to the giant specimens of Anostraca, which Sellier and Morice (1946) have shown to be cytologically similar to normal individuals in one species (*Chirocephalus diaphanus*).

It is difficult to find a suitable measure of the total size of individuals in order that relative proportions of endites, etc. may be compared during growth in different samples. The total length has been shown to be quite useless in preserved specimens (Barnard, 1929; Sømme, 1934; Linder, 1952) and is difficult to measure in living animals, which have considerable powers of contraction. The measurements made on living animals also indicate that there is some increase in length during an instar. Sømme (1934) showed that the median carapace length is more reliable for it is little affected by the action of the preservative.

It has now been possible to show that the growth of the carapace is isometric and is therefore a valid measurement of size at all ages (p. 11).

Unfortunately, the ratio of carapace length/total length varies between samples and so this measurement is valid only in comparisons within a sample.

Generally, *Lepidurus* spp. tend to be smaller than *Triops* spp. and *Lepidurus arcticus* is usually smaller than the rest, but probably more rarely achieves its maximum size than the non-boreal species.

(2) *Colour*

Living Notostraca are frequently brightly coloured, the colours being due to two main pigments within the body and the brown colour of the exoskeleton.

The internal pigments are haemoglobin, which is present in solution in the blood (Régnard and Blanchard, 1883), and a dark blue-green pigment which occurs in connective tissue in many parts of the body; this pigment is of unknown composition, but is similar in nature to that which occurs in some Ostracods (Fox, 1955).

The concentration of haemoglobin varies inversely with the oxygen tension of the medium in which the animal is living (Fox, 1949), and large animals in poorly aerated conditions may have so dense a concentration that the animal appears to be deep red in colour.

The blue-green pigment appears to be more abundant in *Lepidurus* than in *Triops* and the animal is sometimes deep green in colour (hence *Lepidurus viridis*, Baird). In *Triops* it may be completely absent, though a mid-dorsal patch on the carapace and smaller areas on the bases of the thoracic appendages are generally present. It seems to be more abundant in animals which have grown rapidly and under good conditions, when it forms a dark marbling on the carapace and is well distributed elsewhere. The only living specimens of *T. australiensis* that I have seen have been without this pigment, but this is unlikely to have any significance.

The newly hatched larvae of both genera may be densely coloured with a carotenoid pigment, as Fox (1949) reported for *Triops cancriformis*; in successive generations of the same stock the colour of the larvae is very variable and probably depends on the feeding of the parents; well fed females usually contain eggs which are pink with carotenoid, while in starved specimens they are white.

The egg shells of *Triops* are bright red in colour, for a red haemochromogen is present in them (Fox, 1955); this pigment is secreted by the follicle ducts of the ovary, and is brightest in colour in newly laid eggs, becoming duller after they have been dried.

A bright violet pigment occurs in the egg shell of *Lepidurus arcticus* (H. Moore, personal communication), while other species in this genus have eggs of the same colour as in *Triops*.

(3) *Body-length, segmentation, and number of appendages.*

The carapace of Notostraca is attached only to the head region, and the thorax and abdomen are completely free from it; the post-carapace region is divided into a number of segments or body rings, which have considerable powers of telescoping. The first eleven segments, of which the first is incomplete dorsally, normally each bear one pair of appendages ventrally, and together comprise the thorax.

The number of post-thoracic, or abdominal, segments is variable and the series of appendages is continued along them; a few segments at the posterior end of the abdomen bear no appendages.

Linder (1952) has analysed a great deal of North American material and has to a great extent elucidated the relationships between the number of segments, the number of appendages and the number of apodous segments posteriorly. He con-

cludes that the number of segments and the number of appendages are the results of two quite separate growth processes for a number of reasons: the production of segments and appendages in the larvae proceed at different rates; the boundaries of the appendage bearing segments are not complete ventrally; an aberration in which the segments are spiral instead of annular does not upset the arrangement of the appendages; no correlation can be found between the number of appendages and the segments bearing them; and the appendage series may end anywhere along the length of a segment.

While studying the development of the systematic characters during growth I found that the larvae of *Triops* complete their segmentation by the 5th or 6th instar, but that the series of appendages continue to increase and encroach posteriorly on to fresh segments until the 8th or 9th instar, after which the number of apodous segments remains constant. After this the number of appendages may continue to increase for a few instars but come to occupy no further segments. So after the 9th instar the number of segments and the number which are apodous may be taken as fixed in an individual, so that these could validly be used as characters in animals of more than 3–4 mm. in median carapace length.

The total number of segments varies in *Triops* from 32–44, and in *Lepidurus* from 26–34; these results are based on the museum material combined with information from the literature. Throughout this paper the figures given do *not* include the telson which is considered to be post-segmental, and incomplete segments are included in the count.

The figures for *Triops* show that the variation is continuous throughout its range, and separation into groups on the number of segments would be quite arbitrary; the results for females from all sources illustrates this—

No. of segments .	32	33	34	35	36	37	38	39	40	41	42	43
No. of occurrences .	24	31	19	12	11	17	22	12	13	15	10	7

The bottom row of numbers—the number of occurrences—is obtained by counting the number of samples in which each segment-number occurs; this prevents undue weight being given to large samples, which are not evenly distributed along the range of variation.

The apparent bimodality of these figures is due to the fact that one species—*Triops cancriformis*—has a range of segment variation which covers only a part of that of the other species. This species occurs in Europe and naturally predominates in the collections, thus increasing the number of occurrences at the lower end of the scale. *T. cancriformis* has a variation of 32–35, while the other species probably run from 32–43.

By far the greatest number of *Lepidurus* examined fall within the range of 25–29 segments; I have seen only two samples with more, *L. lynchi* Linder and *L. batesoni* sp. n. This is in accordance with Linder's findings, for he suggested that there might be two groups of species within *Lepidurus* based on the number of segments.

The variation within samples bears out the theory that the number of segments may be of use in the systematics of *Lepidurus* but not of *Triops*; in the pure line of *T. cancriformis* there was a variation of 3 in this character (33–35), and variations

of 2, 3, or 4 are usual in samples of preserved specimens. In *Lepidurus*, however, possibly because there are fewer segments, the variation is smaller, rarely being more than 2 in each sample, many samples showing none.

The number of appendages confirms the above grouping of *Lepidurus*; the shorter bodied group has from 35–48 appendages, the longer from 39–71; these figures are based on Linder's data with the addition of counts made on the material I have examined. But in *Triops* I can find no correlation between the number of legs and the number of segments, for high numbers of appendages occur in both short and long bodied specimens, and the converse is also true. In this genus I can find no significance in the numbers of appendages.

The number of apodous segments is a secondary character depending on the interplay of the processes which control appendage and segment formation (Linder, 1952). This is confirmed in my data, most commonly with males and females from the same sample; the males tending to have a smaller number of appendages, the same number of segments and so a higher number of apodous segments than the females. Similarly, *Lepidurus bilobatus* has 33 segments, 60 pairs of appendages and 6 apodous segments (Linder, 1952), while *L. batesoni* with the same number of segments, but only 39–52 appendages, has 8–9 apodous segments.

The apodous segments were frequently counted in early descriptions of Notostracan species, and several specific distinctions have been based on small differences in this number. It is now known that there is so much variation in this character in *Triops* that it is useless as a systematic character; the pure line *T. cancriformis* had a variation of three (5–7). It may be valid in some *Lepidurus*, and is of use in at least one specific distinction.

A few general rules can now be drawn from the data on segmentation and appendage number.

In both genera males often have a higher number of segments within a sample, while the reverse appears to be unknown. In 25 samples of *Triops* I found this to be the case, while in 21 the difference was insignificant.

Certainly in *Triops*, and probably in *Lepidurus*, the males tend to have fewer appendages and so a higher number of apodous segments than the females; in 44 *Triops* samples the males had a higher number of apodous segments, in 7 there was no difference and in 1 the female had more.

Specimens with high numbers of segments tend to have a high apodous number in both genera.

Thus, it is obvious that these characters can be used in systematics only with a great deal of caution, and appear to be of more use in *Lepidurus* than in *Triops*.

(4) *Carapace*

The shape and size of the carapace in Notostraca varies considerably and the differences found have frequently been used in the past by systematists to distinguish species. Ghigi (1921) used the carapace shape as one of his arguments in separating *Triops* into two genera: *Thriops* and *Proterothriops* (*sic*); Barnard (1929) considered the shape to be a distinguishing feature between South African species of *Triops*, particularly between his *Apus numidicus* and *A. namaquensis*. On

the other hand, Linder (1952) made no use of the carapace size and shape in his revision of the North American forms. The carapace is one of the structures which is usually described adequately in the earlier papers.

In each individual the growth of the carapace from the earliest larva is probably isometric; a number of individuals of *Triops cancriformis* and *T. granarius* were measured during the whole of their growth period and it was found that the ratio of

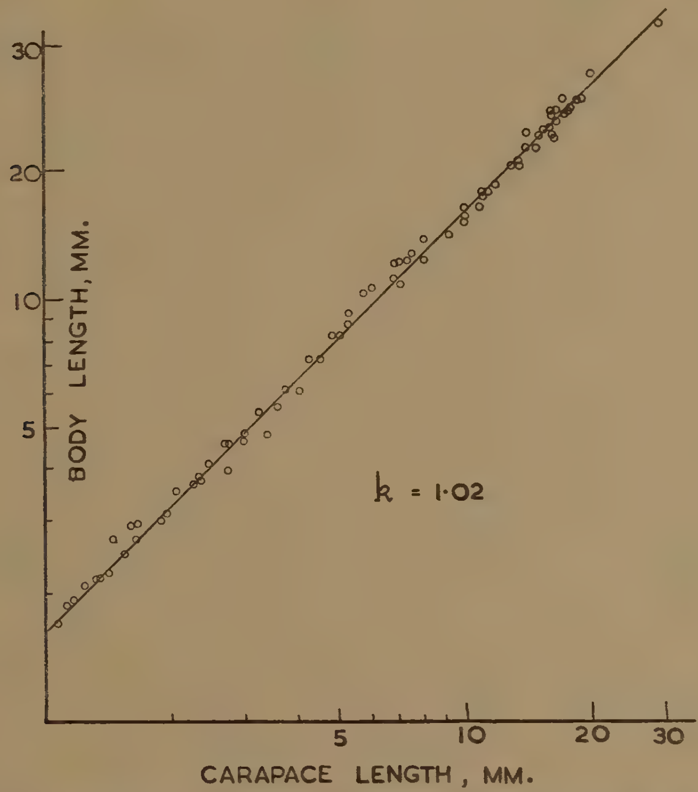

FIG. 1. Growth coefficient (k) of females of *Triops cancriformis* from Hampshire—five individuals.

carapace length to total length remained the same throughout growth. In the former species the growth coefficient (k) of the carapace was 1·02, while in the latter species $k = 1{\cdot}01$; these results are shown graphically in Text-fig. 1.

The basic variation in the carapace is its size relative to the total length of the animal; in some forms it covers a much greater length of the body than in others; correlated with this relative size-difference are other differences in shape and strength

of the carapace ; in those specimens in which it is relatively small it is always more rounded in outline, flatter, and less strong than in those in which it is large. These differences hold good for both genera.

The relationship between carapace length and total length depends both on changes in size of the carapace—the number of segments that it covers—and on changes in the number of abdominal segments. A comparison between two species of *Triops* made on the living animals illustrates this ; British female *T. cancriformis* have about 33 segments of which about 19 are exposed behind the carapace, which thus covers some 14 segments ; *T. granarius* from Johannesburg have, in the female, about 38 segments of which 27 are exposed, so that in this species the carapace covers about 11 segments. In the second species the increase in the number of exposed segments comes both from a shorter carapace and a larger number of abdominal segments. It is impossible to make such calculations on preserved specimens with any accuracy, because of contraction in the preservative.

The carapace appears to cover about 11–14 segments in most specimens, for on these segments are borne the most anterior of the spines which occur on the margins of the segments in the exposed portions of the abdomen ; in all the specimens examined, the first of these spines appear on segments 11–14, regardless of the total number of segments present.

Within a species, males have smaller carapaces than females, although this dimorphism is less marked in *Lepidurus* than *Triops*, and in shorter bodied than in longer bodied specimens of the latter genus. This sexual dimorphism in the carapace has been noted by many authors.

The dependence of the degree of this dimorphism on the number of segments means that while it is usually possible to distinguish males from females at a glance on this character within a population, males from short bodied populations may actually have longer carapaces than females from populations with high segment numbers. In the forms with the lowest numbers of segments the dimorphism may be so slight as to be virtually non-existent.

The carapace is smaller, more round, and flatter in populations of both genera which have relatively high segment numbers ; this is especially well marked in *Triops* where the specimens with the highest numbers of segments have remarkably small carapaces (Text-fig. 2).

Barnard (1929) maintained that the shape of the carapace was an absolute difference between his *Apus numidicus* and *A. namaquensis*, which he found in the former species to be oval in shape and in the latter almost round ; he also gave data on the number of apodous segments which show that *A. namaquensis* is longer in the body than the other species, although some overlap occurred between the two. He was concerned only with South African material, but on examining specimens of these species—and of synonymous ones—from the whole of their range in Africa and Asia I find that there is no discontinuity in the variation of carapace-shape. The round carapaces and the oval are connected by populations of intermediate form (Text-fig. 2A–E). The differences that Barnard found were differences between the long and the short bodied forms of the same species.

I can find no differences in the carapace shape or size which are not correlated

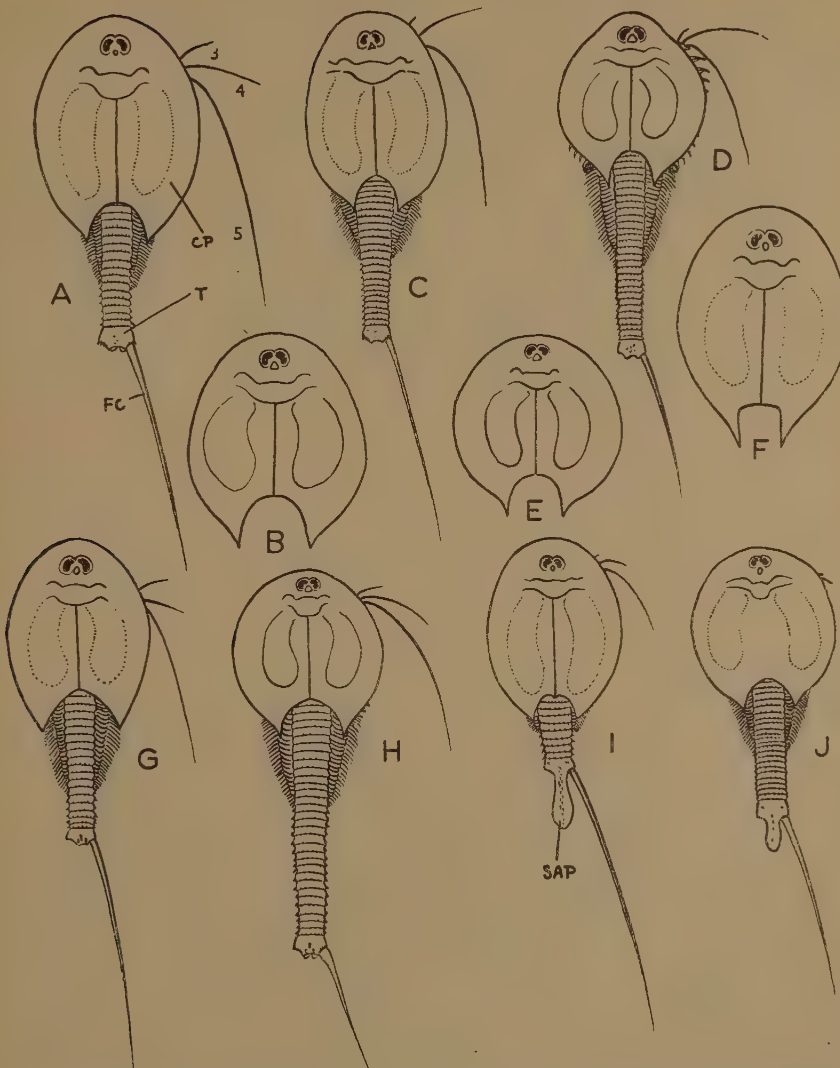

FIG. 2 Correlation of form with number of segments. A–E, *Triops granarius*, progressive increase of segments (32–42) ; F, squared sulcus on some specimens of *T. granarius* from South Africa ; G–H, *T. longicaudatus*, few and many segments respectively ; I, *Lepidurus apus* ; J, *L. batesoni*. (3, 4, 5, = endites of first thoracic appendage, *cp* = carapace, *t* = telson, *fc* = furca, *sap* = supra-anal plate).

with sex or the number of segments; *Triops cancriformis* tends to have a lower number of segments than *T. granarius* and so its carapace tends to be longer, less flat, than in the other species; and specimens of *T. granarius* with a low number of segments have carapaces similar in shape to those of *T. cancriformis*. *Lepidurus* spp. tend to have even shorter bodies and here the carapace may cover most of the abdomen, and may be so deep as to enclose the animal laterally.

The shape of the sulcus, or posterior emargination, of the carapace has frequently been described and importance attached to it; I find it to be very variable and can see no correlation with other characters; it may be shallow and wide in both long or short bodied forms, or small and round in similar animals. A peculiar squared sulcus has been seen in several short bodied populations of *Triops granarius* from Africa (Text-fig. 2F), but this grades into more rounded forms and is obviously of no significance. Wide, shallow sulcus shapes occur most frequently in *T. longicaudatus*, but this is of very doubtful value in the systematics.

The difficulty of an accurate classification of sulcus shapes makes it unlikely that this will ever be a useful character.

(5) *Carapace armature*

The carapace bears an armature of spines both scattered and localized. The whole outside surface may be smooth, or may bear scattered upright spines; the dorsal carina frequently ends in a spine and may bear smaller spines along its length; the sulcus generally bears a row of marginal spines, and the outside edge of the carapace may bear a similar row.

The carapace armature shows a great deal of variation, and has been referred to very frequently in past descriptions; some of this variation does seem to be of use systematically, but it must be used with caution and only as a confirmatory character in most cases.

The armature as a whole varies in its strength and development even within a population, and in some animals the whole armature is more strongly developed than in others—in the former not only are the spines larger and stronger, but they are also more numerous. In *Triops granarius*, when the scattered surface spines are well developed, the sulcus spines are particularly strong, the carina is denticulate and the whole carapace is more rigid than in other specimens. In a population of *T. cancriformis* from Tunisia (MNHNP) the armature of the exoskeleton is extraordinarily weakly developed, though typical of this species in arrangement, and extreme examples in this sample have no carinal or sulcal spines at all—a most singular condition.

The scattered spines on the surface of the carapace were features used by Sars in the description of two species of *Triops* (*Apus trachyaspis* and *A. sculleyi*, Sars, 1899), but Barnard found that specimens bearing such spines occurred sporadically among South African material. I have found such specimens in samples of *Triops granarius* and *T. longicaudatus*, both as isolated individuals and as complete samples. Specimens in which this character is well developed are so conspicuous—the carapace having a prickly feel—that I shall refer to them as the *trachyaspis*-form of whichever species is involved.

The terminal spine of the carina is most prominent in larval *Lepidurus*; I have seen specimens of *L. arcticus*, *L. apus apus* and *L. apus viridis* in which it is relatively enormous in the second and third instars (Text-fig. 13A). In larvae of *Triops* it develops later and is never as large as in young *Lepidurus*. The growth rate of this spine in *Lepidurus* must be strongly negatively allometric, for although it is present in most adults, it is relatively very much smaller in these than in the larvae ; in *Triops*, when it occurs, this spine has a positively allometric rate for it is quite small when it first appears, and becomes, in the adult, of a size relatively similar to that of adult *Lepidurus*.

This terminal spine occurs in almost all adult *Lepidurus* and is absent in only a few. There appears to be no correlation between its absence and other characters ; *L. batesoni* and some specimens of *L. apus apus* and of *L. apus lubbocki* are without it, but these specimens of *L. apus* are otherwise quite normal. There is probably a variation in the growth rate of this spine to account for its disappearance in adults of a few populations.

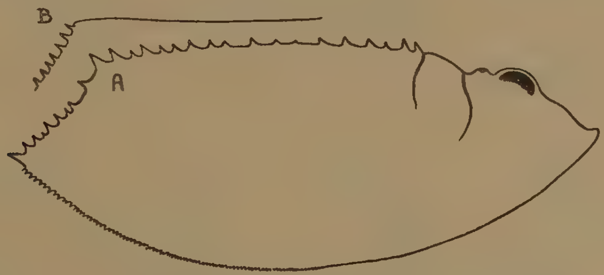

FIG. 3. Carapace of *Lepidurus lynchi*. A, typical form of carinal spines ; B, specimen with no carinal spines.

In *Triops* there is a loose correlation between the occurrence of the terminal spine and other characters ; within a species it is more commonly present in short than in long bodied forms. There is some difference between species, too, and as might be expected it is almost always present in the relatively short bodied species, *T. cancriformis*. It is present in the remaining species only in their short bodied forms.

The carina may bear a series of spines, most commonly at the posterior end just anterior to the terminal spine. These have frequently been used in the past for systematics (Ghigi, 1921 ; Linder, 1952) and they have proved to have value in certain cases. In *Triops* they may be present, or absent, in both long and short bodied forms, but there are some interesting differences within *T. cancriformis*. In this species a few small spines are generally present posteriorly, and these are more numerous and much stronger in specimens from Morocco and Southern Spain ; these are the populations referred to by Ghigi (1921) as *Thriops mauretanicus*, but they are now considered to comprise a sub-species (sens. Mayr, *et al*) of the more wide-spread *Triops cancriformis*. Another sub-species of this species is characterized by the complete absence of carinal spines.

In *Triops australiensis* and *T. longicaudatus* these spines are most frequently

completely absent, but in a number of populations, that from the rice fields of Biggs County in California, for example, the whole carina bears an even row of very small denticles.

Most specimens of *Triops granarius* are without carinal spines, and only a few of the short bodied specimens have an arrangement like that of *T. cancriformis*. Very rarely this species has a long row of very small denticles like those of *T. longicaudatus*.

The majority of specimens of *Lepidurus* have perfectly smooth carinae but a remarkable series of large teeth along the carina occurs in *L. lynchi*, quite unlike anything else in the Notostraca (Text-fig. 3).

The sulcus normally bears a marginal row of spines, the only exceptions being some of the specimens of *Triops cancriformis* from Tunisia mentioned earlier. There is a fairly clear correlation of the form of these spines with the number of segments in *Triops*, but not in *Lepidurus*; they are larger and fewer in number in short bodied forms of the former genus.

Their development in *Triops* is fairly clear; the spines at the outside angles of the sulcus appear first, in the 4th or 5th instar, at which time the rest of the sulcus has a finely granulated margin. The first marginal spines appear in the 7th or 8th instar, and increase in number until about the 10th instar, after which time the number is fixed, though in a few specimens small subsequent additions may occur. There is little variation in this character in an individual after it is about 5·0 mm. in carapace length.

Barnard (1929) considered that there was so much variation between individuals in the sulcus spines that their use in systematics was not justified, although earlier writers had placed much emphasis on them. Linder admitted this variation, but thought that in some cases specific differences could be found.

I can discover no differences of the sulcal spines in *Triops* which can have any value in systematics, most of them are correlated merely with body length; in *T. granarius*, short bodied forms have long, slightly curving spines and in longer bodied animals a larger number of small, blunt spines occurs. As in other characters *T. cancriformis* here resembles the shorter bodied *T. granarius* specimens.

In *Lepidurus*, a correlation with body length was not observed; some specimens with 28 and some with 33 segments had small squat spines, but the vast majority of samples of all body lengths have long spines similar to those of *Triops cancriformis*. An unusual arrangement occurs in *Lepidurus apus packardi* in which the margin is closely set with many small squat spines like those of larval *Triops*.

The outer margin of the carapace in both genera normally bears a series of denticles which produce a finely serrated edge; this is variable in development, and is normally stronger near the posterior angles of the carapace; in only one case are these marginal denticles of any value systematically; some specimens of *Lepidurus lynchi* bear a series of teeth along this edge which are very much larger than those of any other known form.

The amount of individual variation which may be expected in the carapace armature of a population was illustrated by the pure line of *Triops cancriformis*; here the number of posterior teeth on the carina varied from 2–10, the number of sulcus spines from 24–32, and all the specimens had a large terminal carina spine.

(6) *Supra-antennal crest*

On either side of the ventral surface of the head there is a ridge, behind which is set the first antenna ; this is the supra-antennal crest of Simon (1886), which Linder (1952) suggests may be worth study. I find it variable within a single species, in some specimens of *Triops c. cancriformis* it is denticulate and in others smooth and less prominent. It seems improbable that it is of importance systematically.

(7) *Eyes and dorsal organ*

In all adult Notostraca the dorsal surface of the head bears a pair of compound eyes, an ocellus, and the dorsal (or nuchal) organ.

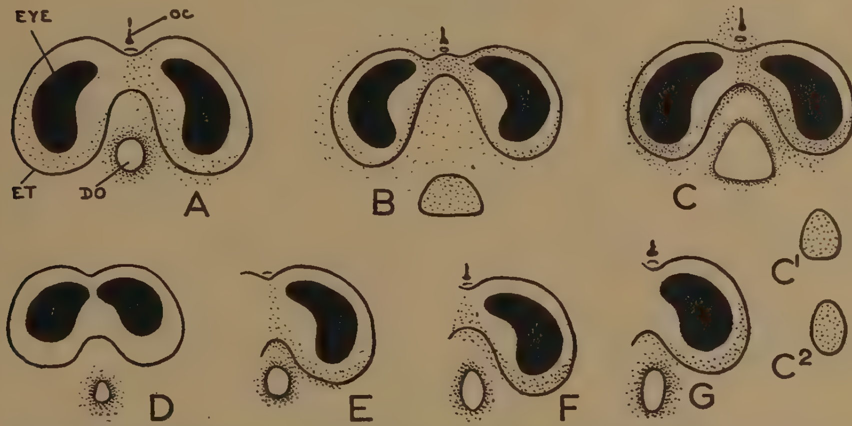

FIG. 4. Eyes and dorsal organs. A, *Triops cancriformis* ; B, *T. australiensis* ; C, C_1, C_2, *Triops granarius* ; D, *Lepidurus batesoni* ; E, F, *L. apus* ; G, *L. arcticus*.

The size and arrangement of these structures are given in most specific descriptions and considerable importance has been ascribed to them, in particular to the dorsal organ ; Barnard (1929) showed that the dorsal organ varied in South African material from a small round shape to a larger and triangular one. Further, he found that the small, round dorsal organs tended to be set on a tubercle in his animals, but that the triangular ones were less elevated and nearly flush with the surface of the head. These differences, to which he ascribed much importance in separating species, now appear to be another example of a character which is correlated with the number of segments, and which varies in a similar fashion in several species.

In all the species of *Triops* the specimens with a low number of segments tend to have small, round and elevated dorsal organs, and as the number of segments increases so the dorsal organ becomes larger, less elevated, and more triangular in shape (Text-fig. 4C–C_2).

This is well shown by *Triops granarius* ; in specimens from South Africa with only 33 segments the dorsal organ is small and round, or slightly pear-shaped, as it is in

specimens with 36–37 segments from Chufoo, China (both BMNH); in longer bodied specimens it is much larger and more triangular. In *T. cancriformis* the usual shape is round, but in some of the longer bodied individuals it approaches the triangular form of most specimens of *T. granarius*. *T. longicaudatus* is similar in this character to *T. granarius*, but in *T. australiensis* a peculiar wide shape, with a slight emargination of the posterior margin, occurs in a few specimens.

I have seen no specimens, and can find no records, of *Lepidurus* with triangular dorsal organs; here the round shape seems to be usual but in most species it varies from round to oval (Text-fig. 4). In *L. arcticus* a peculiarly long, narrow oval shape is common and this does not appear to occur in other species (Text-fig. 4G).

The growth rate of the dorsal organ is very strongly negatively allometric and this further complicates its use as a systematic character. In the larvae it is a relatively enormous structure so that in the first instar its median length is commonly about half that of the carapace rudiment (Text-fig. 13B).

During growth to adult size its linear increase is only $\times$ 2 or $\times$ 3 while the relative growth of the carapace is naturally very much greater. This negative allometry appears to continue throughout growth.

Linder made use of the relative arrangement of the eyes and the dorsal organ in his species of *Lepidurus*. He found that *L. lynchi* has the dorsal organ placed well behind the posterior boundary of the eyes and of the tubercles over the eyes, in contradistinction to the rest of the genus in which he found that the dorsal organ was placed in part between the eyes. *L. batesoni* sp. n. has the first arrangement (Text-fig 4D), but *L. bilobatus*—the other member of the long bodied group—has not.

In *Triops*, almost all the specimens examined had the anterior margin of the dorsal organ between the eyes, the only exceptions being 8 of the 12 samples of *T. australiensis* examined, in which the arrangement was precisely similar to that of *Lepidurus lynchi* and *L. batesoni* (Text-fig. 4B); in the other four samples it was normal. This may indicate that not too much reliance should be placed on this character in either genus as a primary distinction between species.

(8) *Telson*

The telson bears an armature of spines on both dorsal and ventral surfaces, and variation of these have commonly been used in the past for separating species (Packard, 1883; Ghigi, 1921; *et al.*).

The important spines on the dorsal surface of the telson fall naturally into four groups to which it is convenient to apply names (Text-fig. 5); around the bases of the furca are rings of *furcal* spines; on the posterior margin of the telson of the larvae the first spines to appear are large and are identifiable in the adult—the *posterior marginal* spines; the median area of the telson may bear a row of large spines or scattered smaller ones—the *median* spines; around the dorsal sensory setae are rings or arcs of *setal* spines.

The development, but not the origin, of these spines differs radically between the several species of *Triops* (Text-fig. 5), and the final arrangement is of the greatest importance in the systematics.

All the specimens of *Triops* which were available were examined on a geographical

asis, and no account was taken of previous determinations of the specimens; it ras found that there was a strong correlation between the spine pattern of the telson nd the geographical distribution of the animals, but none with the sex or the umber of segments.

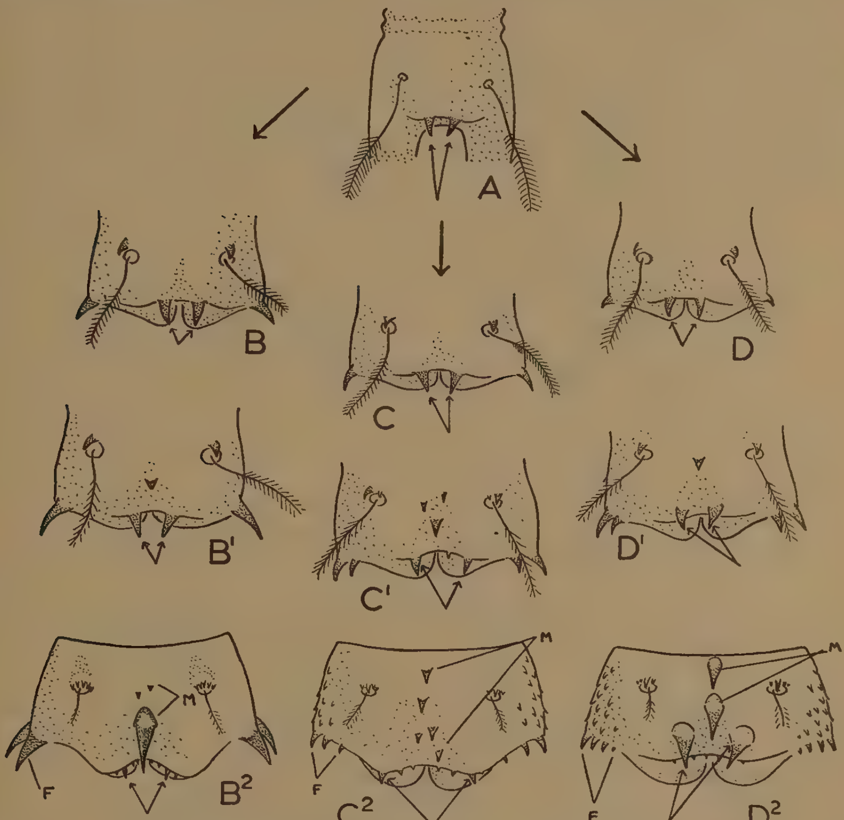

FIG. 5. Development of telson armature in *Triops*. A, larval stage (instar 2) common to all; B, C, D, instar 5–6; B_1, C_1, D_1, 3–4 mm. carapace length; B_2, C_2 D_2, adults. B_n, *T. cancriformis*; C_n, *T. granarius*; D_n, *T. longicaudatus* (the small arrows indicate the position of the posterior marginals in each case; *f* = furcal spines, *m* = median spines).

Without exception the specimens from Europe and western Russia have a small umber of median spines arranged in an accurate row in the centre of the telson, the urcal spines are few and large, and the posterior marginals small, thin and remaining n the margin in the adult (Text-fig. 5A); this pattern occurs also in North Africa, he Middle East and northern India. In Africa south of the Palaearctic Region all

the specimens have a larger number of small, relatively scattered medians in the mid-dorsal region, small, numerous furcal spines, and small posterior marginals (Text-figs. 5C, 6A). This pattern overlaps the European type in North Africa and the Middle East without forming intermediates, and then spreads across Central Asia to the Chinese coast. In North and South America the medians are similar to those of the European form, but there are two large spines, one on either side, at the posterior end of the median row, which represent the enormously enlarged and forwardly migrated posterior marginals, a fact which was confirmed by a study of the larval development (Text-fig. 5D). This form also occurs to the exclusion of others in the West Indies, the Galapagos, Oahu, and Japan; a derivative occurs in New Caledonia (Text-fig. 16).

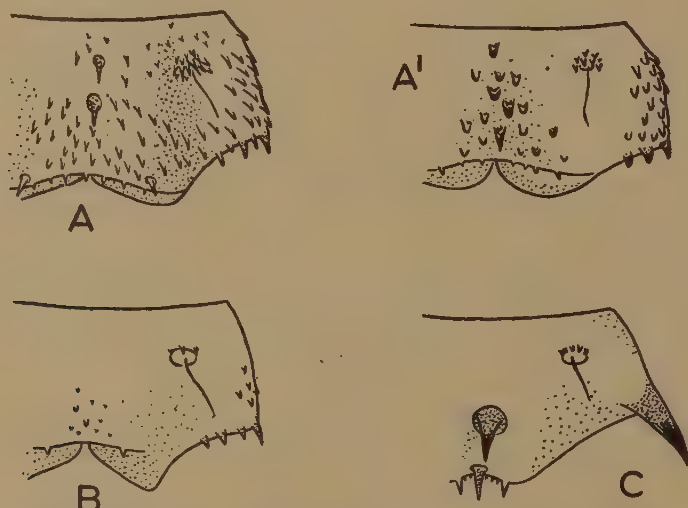

FIG. 6. Telsons of *Triops*. A, *T. granarius* (*trachyaspis*-form); A_1, *T. granarius*; B, *T. australiensis*; C, *T. cancriformis mauretanicus*.

The Australian forms have a very few small scattered medians, as in the African form, but they are so few in number as to be frequently absent (Text-fig. 6B); the rest of the armature is as in the African specimens.

This gives a picture of four large groups which are to a great extent allopatric, but forming where they overlap no intermediates. The descriptions in the literature completely confirm this grouping and are too numerous to list with profit.

As a systematic character this pattern appears to be perfect, there are no known intermediates, it is unlikely that it has any direct adaptive significance, and it is very easily seen in the specimens.

It must be remembered, however, that although the pattern is stable the numbers of spines which form it are very variable; in the pure line *Triops cancriformis* there

were 1–4 medians, 2–4 furcals, and, once, small additional posterior marginals barely distinguishable from the primary pair.

The number of these spines is fixed from a size of about 5 mm. carapace length, but as Text-fig. 5 shows, their relative sizes forming the true adult patterns are not stable until a little later, and allowance must be made for this (e.g. *Apus mavliensis*

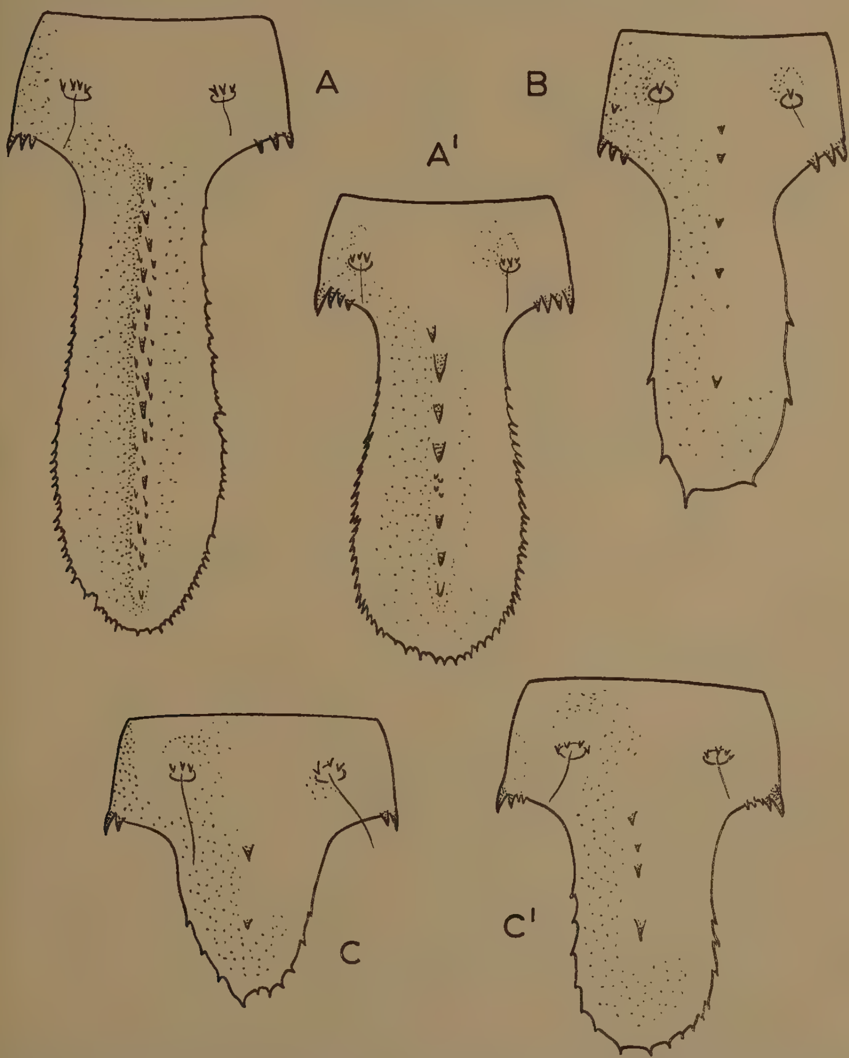

FIG. 7. Supra-anal plates of *Lepidurus*. A, *L. apus apus*; A_1, *L. apus lubbocki*; B, *L. batesoni*; C, ♀, C_1, ♂, *Lepidurus arcticus*.

Tiwari appears to have a different telson pattern from the other Indian forms, but this species was described on immature individuals in which the posterior marginals were still relatively very large).

The spines encircling the dorsal setae are very similar in arrangement, though not in number, in all specimens of *Triops* examined, and no importance is attached to them.

In *Lepidurus*, the spines corresponding to these four groups can be recognized, but they are to some extent modified ; the posterior marginals are the first to appear in the larval telson (*L. apus*) and the posterior margin of the telson on which they are borne expands rapidly to form the supra-anal plate, carrying them with it, and they are soon indistinguishable from the other spines on the margin of the plate in most specimens. The furcal spines are similar to those of *Triops granarius* and do not differ much from species to species ; the setal spines are similar in form and lack of variation to those of *Triops* ; the medians form an elongate row along the mid-dorsal line of the plate.

This median series shows considerable variation and has frequently been used in the separation of species ; the number of spines increases to a certain extent as the animal grows (Linder, 1952) ; and this process probably continues until the animal is at least 15–20 mm. in carapace length, to judge from a sample from Berlin of *Lepidurus apus* (BMNH) consisting of large and small individuals.

The median spines may be borne on a slight keel, which is better marked in those specimens with a large number of spines in this series ; it is impossible to draw a line between presence and absence of a keel and contrary to Linder's opinion, I can make no use of it.

The number of spines in the median series is useful in the systematics of *Lepidurus* species, serving to distinguish the nominate race of *L. apus* from the other three sub-species. *L. arcticus* has a much lower number than the rest of the genus. These differences are not connected with the relative size in the adults of the supra-anal plate ; both *L. arcticus* and *L. lynchi* have relatively low numbers of medians, although the former has the smallest supra-anal plate in the genus and the latter one of the largest.

The marginal spines of the supra-anal plate vary in size and number and there is a connection between them and the median spines, when the latter are small and numerous, so are the former ; the marginals therefore are relatively large and sparse in *Lepidurus arcticus*, *L. lynchi*, and *L. batesoni* compared with the other species.

The size of the supra-anal plate itself varies between species—the most obvious difference being in *Lepidurus arcticus* where it is very small—but a great deal of the observed differences are due to age and sex ; males (Text-fig. 7C) have relatively longer and more spatulate supra-anal plates than females (*L. apus*, Braem 1893 ; *L. arcticus*, Sømme 1934) ; and the structure has a positively allometric growth rate throughout the period of growth (Braem, 1893 ; Campan, 1929).

The end of the plate is occasionally incised medianly, giving it a bilobed appearance ; this appears in several species and has no importance (Linder, 1952), and it is to be expected that this will occur in species other than those in which it has already been recorded.

The shape of the telson was used by Packard (1883), but Linder has shown that this is an unreliable character in *Triops*, though he records relative differences in length and breadth in some *Lepidurus* species. The variation is such that no reliance is placed on it here.

The dorsal sensory setae are present, and similar in form, in all species of Notostraca that I have examined, and are longer in small than in large specimens.

(9) *Segmental armature*

Each segment which is exposed behind the carapace bears a series of spines on its posterior border; this series is interrupted by the appendages and is continued ventrally only on the apodous segments.

The form of these spines on the ventral surface of the apodous segments has frequently been used in the systematics of both genera; Ghigi (1921) considered them to be important in *Triops*, as did Linder (1952) in *Lepidurus*.

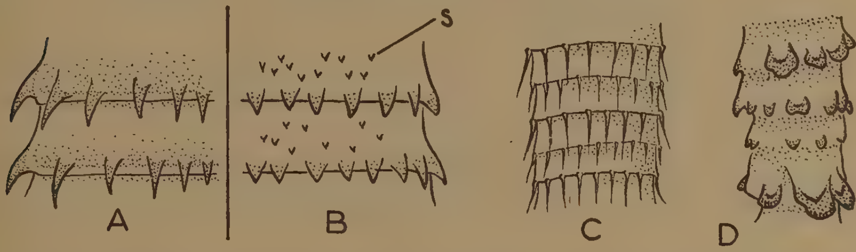

FIG. 8. Armature of apodous segments (A, B) and furca (C, D) of *Triops*. A, *T. cancriformis* without supernumeraries; B, *T. granarius* with supernumeraries (s); C, ♀ *T. cancriformis* or *granarius*; D, ♂, *T. granarius*.

On the ventral surface of these segments the spines near the midline are usually smaller and set more closely together than the lateral ones. Linder (1952) considers that the number and relative size of these centrals is diagnostic of certain species; he gives a variation of 13–28 teeth in *Lepidurus packardi*, *L. couessi*, and *L. bilobatus*, and only 8 in *L. lynchi*; I find the variation so great that this character is effectively useless even though the differences are at times striking.

In *Triops*, the shape of the marginal spines was used by Ghigi (1921), who found that they were squat in his *T. mauretanicus*, and finer in his other species; I find that the European and North African material—which Ghigi divided into species—shows continuous variation in this character although, as he described, there is a tendency for the Moroccan specimens to have squat spines.

These spines become rounded and heavy in males of *Triops granarius* in which the ventral armature of furca and telson are heavy; they are thus heavier in males than in females of the same species.

A more useful character on the apodous segments is the presence or absence of scattered supernumerary spines which occur between, and anterior to, the marginal spines and are much smaller than them (Text-fig. 8). In *Triops cancriformis* only one

specimen has been seen which possesses any of these spines, a female from Palestine (coll. Goldschmidt) which had 3–4 small supernumeraries on one of the apodous segments. In the other species of *Triops* it is most unusual to find a specimen which does not possess at least a few supernumeraries on each apodous segment, and in the main there are 10–12 per segment.

I have not seen these spines in *Lepidurus*.

(10) *Appendages*

The appendages have been described in considerable detail for one species (*Triops cancriformis*, Lankester 1881), but with the exception of one character have been little used in systematics. The endites of the first thoracic appendage are drawn

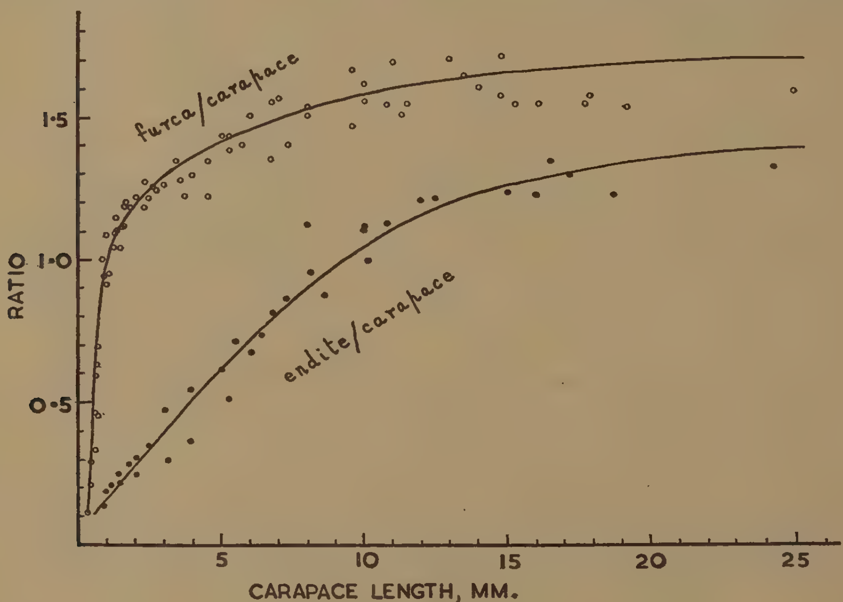

Fig. 9. Relative growth rates in *Triops cancriformis* from Hampshire. Furca and longest endite of first thoracic appendage expressed as ratios furca/carapace and endite/carapace for various carapace lengths. Any slope on the line thus indicates allometric growth, since the growth rate of the carapace is isometric.

out into filaments of which the longest endite (the fifth) forms an antenna-like structure in most forms. The length of the endite 5 and the number of segments of which it consists have been described by too many past authors to list. Even recently small differences in endite length have been considered to have significance (Tiwari, 1952).

A study of the developing endite of *Triops cancriformis* and *T. granarius* has shown

hat it grows positively allometrically and that this rate continues, to some extent, hroughout life (Text-fig. 9). So small differences in relative length are of no use n systematics without much more investigation of the growth rates of this structure n many populations.

It is likely that the length of the endites is not related to the size of the animal *er se*, but to the instar that the animal has reached. Specimens which have grown apidly, with a large increment at each instar would have a different endite length t a particular size from individuals with low instar increments due to poor condiions; this is borne out by the great size and relative proportional differences een in laboratory cultures.

In museum samples, perhaps for this reason, the individual differences in this haracter appear to be greater than those to be expected between large and small pecimens; if a sample is arranged in order of carapace-length the endite/carapace atio does not increase evenly up the series, as would be expected from the results btained from the growth of single specimens, and the inference to be drawn must e that the specimens have grown at different rates and are of different sizes at ach instar.

This is further supported by the occurrence of two samples taken from the same ocality in different seasons; two such samples from a locality in the Saône area of rance (MNHNP) collected two years apart consisted one of large, the other of mall adult individuals, but the endite/carapace ratio was very similar in each; in he first, individuals of 29–31 carapace length had a carapace/endite ratio of 0·80–·84; in the second sample the same ratio occurred in specimens of 9·5–10·8 mm. n length.

The situation is further complicated by the fact that there is sexual dimorphism n the endite length; in 26 bisexual samples of *Triops*, 24 showed higher endite/arapace ratio in the males. This may be due to the relatively shorter carapaces of nales than to any real difference in endite length relative to the total size of the nimals. In living specimens this appeared to be the case.

It is very noticeable that the endites are shorter relative to the body length in oth sexes of the longer bodied forms, but it is not possible to give reliable figures or this because of the parallel differences in the relative carapace length which enders inter-sample comparisons very difficult.

The range of the endite/carapace ratio is very great within a species determined s such on other characters; in *Triops cancriformis* this varies from 0·55–1·28, and n *T. granarius* from 0·47–1·52. No correlation with the geographical distribution ould be found.

In *Lepidurus* the endites are not as long as in *Triops*. *Lepidurus arcticus* and *L. pus* form a series from animals with very short endites which scarcely project eyond the carapace, to those in which they are relatively long. In *L. batesoni* the rrangement is unique; the 5th endite of the first appendage is little longer than hat of the second appendage, and the 6th endite forms a claw in both appendages lthough in all other Notostraca it is reduced to a small, soft lobe at the base of the th endite in the first thoracic appendage, undergoing negative allometry during rowth (Text-fig. 10).

Linder (1952) remarks " . . . the legs of various species are known to be very similar to each other . . . "; I can find no reference to a comparative study of the appendages of Notostraca, and so it seemed valuable to attempt at least a preliminary survey. Unfortunately, it is necessary to dissect the appendages from the specimen

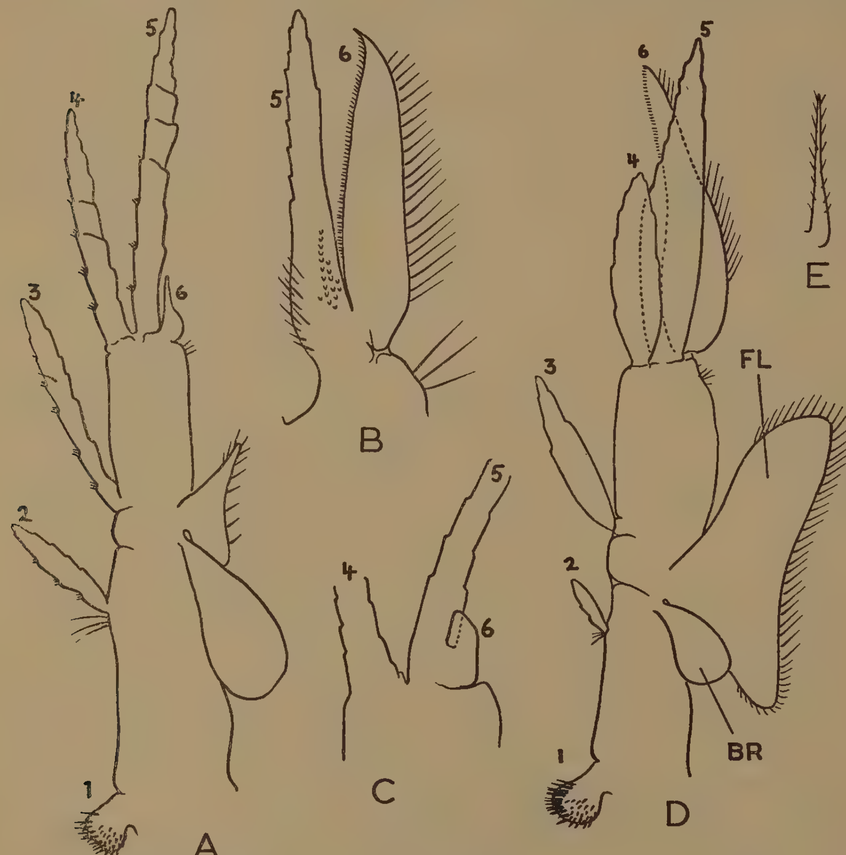

FIG. 10. Thoracic appendages: A, first thoracic appendage of *Lepidurus arcticus*; B, tip of second thoracic appendage of *Triops cancriformis*; C, tip of first thoracic appendage of *T. cancriformis*; D, first thoracic appendage of *Lepidurus batesoni*; E, endite 6 of first thoracic appendage of larval *Triops cancriformis*. (numbers = endites, *fl* = flabellum, *br* = bract.)

in order to examine them properly, and this has naturally been possible with only a few specimens. Appendages of representatives of both sexes of all four species of *Triops*, and of several of *Lepidurus* were examined after mounting in polyvinyl lactophenol.

The first antenna is present in all larvae and adults and is remarkably uniform
ı structure ; it bears at its tip three setae in all species that I have examined, though this number may be apparently altered by breakage. An aberration was
en in one specimen out of a sample of a *trachyaspis* form of *Triops granarius* from
outh Africa in which a pair of additional strong spines were present on one
argin.

The second antenna must be present in all larvae, for in them it is the main
comotor organ ; the form and numbers of setae are identical in the larvae of all
ur species of *Triops*, but I have been unable to make comparisons in *Lepidurus* ;
ıis appendage subsequently dwindles, due to negative allometry, and its locomotor
ınctions are taken over by the thoracic appendages. It is often absent in large

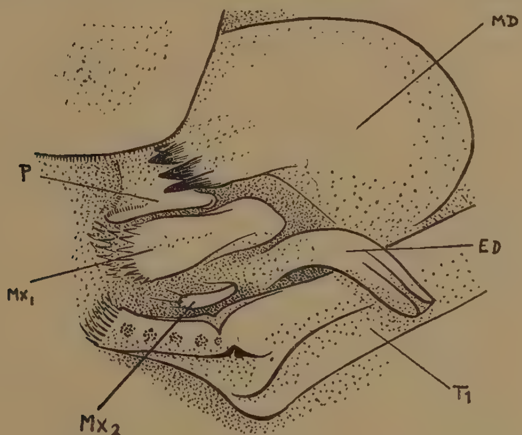

FIG. 11. Mouth parts of *Triops cancriformis* to show second maxilla. (*md* = mandible, *Mx*1 = first maxilla, *Mx*2 = second maxilla, *p* = paragnath, T_1 = first thoracic appendage, *ED* = efferent duct of shell-gland).

ecimens, or it may be present (but very hard to detect) in the cleft in front of
ıe mandible. I have found both conditions in large individuals of all species and
ın attach no importance to its presence or absence, contrary to the opinions of
inder (1952) and Spencer and Hall (1896).

Ghigi (1921) used the arrangement and relative sizes of the teeth on the triturating
ırface of the mandible as a systematic character in his division of European and
orth African material ; I have examined this character in many specimens con-
ecific with his material and there is so much variation that the invalidity of the
ıaracter seems certain. Gauthier (1934) and Pérès (1939) found similar variation
ı their North African material.

The first maxilla has never been described comparatively ; I find the main varia-
on to be in the row of spines on the ventral edge of the appendage. These tend to
e fewer in number and finer in *Triops cancriformis* than in the other species in the

genus, but there is probably a complete gradation of intermediates, and I can make no use of the appendage in the systematics.

The second maxilla has received more attention than the previous appendage and seems to provide an important character (Text-fig. 11). Sars (1901) noted that the second maxilla was larger in *Lepidurus* than in *Triops*; this is so, and this appendage is also larger in *T. cancriformis* than in the other species of the genus, but even in this species is so small that it can scarcely be of importance in the feeding mechanism. Linder (1952) reported that it was absent in large individuals of most species of *Triops* (*australiensis*, *granarius*, *numidicus*, *longicaudatus*), but that no dwindling occurred during growth in *T. cancriformis*. I cannot agree with this. The second maxilla is present in all samples that I have seen of *T. cancriformis* and *T. granarius*, and absent in all those of *T. longicaudatus* and *T. australiensis*. Even in very small specimens of the latter two species it is absent; in a narcotized female from Morawa in Australia it was clearly missing, yet this specimen was only 7·5 mm in total length.

In those species of *Triops* in which it is present it does not dwindle during growth in a *T. cancriformis* of 8·0 mm. carapace length the second maxilla was 0·2 mm. long and in one of 18 mm. carapace length it was 0·4 mm. long; in a *T. granarius* of 7·5 mm. carapace length it was 0·13 mm. long, and in one of 13·8 mm. it was 0·33 mm.

Thus, the presence or absence of a second maxilla provides a clear character separating two species groups within *Triops*, but it is present and well developed in all species of *Lepidurus*.

The efferent duct of the maxillary gland arises at the base of this appendage, or from the position of the base if the appendage is absent; this duct is longer in *Triops* than in *Lepidurus* (Sars, 1901) and longer in male than in female *Triops*, in all the bisexual samples that I have examined.

The endites of the first thoracic appendage have already been dealt with, and I could find no significant variation in the other lobes of this appendage, except that the flabellum was relatively larger in *Lepidurus batesoni* than in other species—another character of the 2nd thoracic appendage appearing on the 1st in this species.

In the second thoracic appendage, the form of the terminal " claw " (= exopodite, Lankester 1881; apical lobe, Borradaile 1926; endopodite, Linder 1952; which I shall call endite 6 from the precisely similar ontogeny in the early stages of this and the other endites) was used by Ghigi (1921) to differentiate between species of *Triops*; I find great variety in the form of this lobe, but none that can be correlated with other characters. The relative lengths of endites 5 and 6 of this appendage show a sexual dimorphism; in males endite 5 is commonly longer than endite 6, while in the females they are more nearly equal. This is well known and I have been able to confirm it in all the bisexual samples that I have seen.

In the remainder of the thoracic series there is considerable variation in the shapes of the lobes of the appendages, but I can find none that are of importance between species; however, all the specimens that I have seen of *Triops granarius* from Central and Eastern Asia have endite 6 of the mid-thoracic appendages of a more rounded shape than is usual.

The armature of these appendages shows much variation in numbers of spines

ut not in their arrangement—a situation common in the armature on other ructures in these animals. The numbers of spines in any group tend to increase uring growth, but I have not been able to follow this closely.

The abdominal appendages showed no differences which might be of use systematilly except to demonstrate once again a similarity between *Triops cancriformis* and e *Lepidurus* species ; the flabellum of *Lepidurus* bears a number (20–30) of setae round its outer margin, and these are reduced in number in *Triops*. But *T. cancrirmis* has a higher number (10–20) than the other species (e.g. *T. granarius*, 4–9). Linder (1952) mentions an inflated condition of the flabella in some specimens ; is I find to be due to post-mortem changes, especially in those animals which have ied just after moulting, when the flabella are commonly so turgid with fluid after a w hours that they have the appearance of small red balloons.

I) *Furca*

The length of the furca has been considered an important systematic character nd was often included in even the early descriptions, but recent authors have thought unreliable (Linder, 1952).

The furca grow very rapidly in the larval stages of *Triops* but their positive lometry soon becomes less marked, though some relative increase probably occurs roughout life (Text-fig. 9). The furca are generally relatively longer in those ecimens in which the endites of the first thoracic appendage are long, and are robably correlated in their development with the number of segments in the same ay as the endites. That there is no direct correlation with the endite length is own by *Lepidurus arcticus* in which the endites are very short, but the furca are milar in length to those of the other species.

Gurney (1924) showed that sexual dimorphism in the armature of the furca curred in *Triops* ; the spines on the ventral surface of the proximal region of the rca tend to be broader in males than in females, in extreme cases forming proberant scales (Text-fig. 8C, D). With few exceptions this dimorphism is more arked in long bodied forms, where the base of the furca tends to be relatively thick nd rapidly tapering. In *Lepidurus* these spines are a little, but not much, thicker males than in females.

PROTEIN SPECIFICITY

Oxyhaemoglobin has a characteristic absorption spectrum, and small differences the wave-length at which the axes of the absorption bands occur have been emonstrated for several species of *Daphnia* by Fox (1945, 1946) ; similar ifferences in the position of the absorption band axes of the chlorocruorin of species nd varieties of *Sabella* have been used systematically by the same author (1946).

The blood of Notostraca contains a considerable concentration of haemoglobin solution and the size of the animals is such that a volume of blood sufficient for ectroscopic analysis can readily be withdrawn by a micro-pipette. It seemed rofitable to determine the wave-lengths of the absorption bands of as many opulations of Notostraca as were available, and to apply the results to the ystematics.

A Hartridge reversion spectroscope was used to determine these wavelengths, in the manner described by Fox (1945), with a small refinement in technique to eliminate personal bias and errors due to parallax; the operator kept his eye to the instrument throughout a series of measurements and an assistant made the readings on the micrometer head and noted them down.

The wave-length of the axis of the oxyhaemoglobin-α band was determined by comparison with a sample of blood of similar optical density and of known wavelength (human blood, 5775Å). A number of readings were made on each sample of blood and the results were treated statistically.

Several cultures of *Triops cancriformis* from different European localities were compared, using several adults from each culture. The results (Table I) show that although there is little individual variation, the three populations are apparently different from each other; these differences gave a probability of significance of 0·02 when a *t* test was applied to them, and it may be taken that they are real and not referable to errors in the methods of measuring.

TABLE I.—*Wave-length of the axis of the oxyhaemoglobin-α band. Means of the readings taken on each animal, the averages of these means ($\overline{X}$), the number of readings per sample (N), and the standard errors of the means (S.E.). The figures in parentheses indicate the distribution of the readings within a sample.**

	Triops cancriformis			*T. granarius*		*T. longicaudatus*
	Sweden	England	Italy	Johannesburg	Grahamstown	California
Means per animal (Å)	5779·7 (30)	5778·3 (40)	5777·0 (20)	5776·7 (10)	5778·2 (30)	5777·3 (30)
	5778·9 (30)	5778·8 (30)	5778·2 (30)	5776·4 (30)	5775·5 (30)	5776·3 (30)
	5779·0 (30)	5778·6 (20)	5777·9 (30)	5776·8 (30)	5776·5 (30)	—
	5780·6 (30)	5778·8 (32)	5777·3 (30)	5777·3 (30)	5778·3 (30)	—
	5779·8 (28)	5778·9 (39)	—	5776·9 (30)	—	—
$\overline{X}$ (Å)	5779·6	5778·6	5777·6	5776·5	5777·1	5776·8
N	148	161	110	130	120	60
S.E.	0·356	0·305	0·281	0·340	0·370	0·255

This indicated that inter-specific differences must be considerably greater than these intra-specific ones to be of any value in systematics, and that many populations of a species must be tested before a value characteristic of that species could be determined.

In fact, subsequent inter-specific comparisons gave results (Table I) very little different from those obtained with *Triops cancriformis*.

The span between the axes of the oxyhaemoglobin and the carboxyhaemoglobin-α bands was also examined, for this is known to show differences between species in some cases (Fox, 1946). The results obtained with three species of *Triops* showed no differences which would justify further investigation. (span: *T. cancriformis* = 50·1 Å, *T. longicaudatus* = 48·2 Å, *T. granarius* = 47·5 Å).

The results of both these investigations are of no practical value in the systematics of these animals—the differences being much smaller than those found and used in *Sabella* by Fox—but do serve to demonstrate that in this character, as in others, the species of *Triops* form a remarkably closely related group.

* A single specimen of *T. australiensis* from Kalgoorlie was tested and gave a result of 5779·3 Å.

REPRODUCTION

It has long been known that some populations of Notostraca contain both males nd females, and some only females. The occurrence of large populations in which o males could be found has generally been assumed to indicate parthenogenesis, specially since it was also known that isolated females from such populations could roduce viable eggs.

Bernard (1889) found scattered testis lobes in the gonads of female *Triops cancri-ormis*, *Lepidurus apus* and *L. arcticus*, and reported these occurrences as cases of ermaphroditism. Zograf (1906) found ovarian tetrads developing in the testis

FIG. 12 Testis lobe in ovotestis of *Triops cancriformis*. 5μ section, Carnoy/Feulgen. (*S* = sperms ; *Sc* = spermatocytes ; *F.D.C.* = follicle duct cells).

valls of male *L. apus*, which must surely be an aberration of no use to the animal, or the oocytes subsequently degenerated. Spencer (1896) could find no testis lobes n the ovaries of *Triops australiensis*.

Bernards' findings, largely ignored since his account, have been confirmed in the resent work during investigation of the cytology of *Triops* and *Lepidurus*, and have een reported elsewhere (Longhurst, 1954). Hermaphroditism has been found in hree species—*Triops cancriformis*, *T. longicaudatus* and *Lepidurus arcticus*—and it vas found that females of the first two laid viable eggs in isolation and contained ovotestes (Text-fig. 12) ; no *L. arcticus* reached adult size. Females of *Triops granarius* and *T. australiensis* were unable to lay eggs in the absence of males, but

did so readily as soon as males were put into the tanks with them and pairing ha[d] occurred; this was presumably correlated with the fact that no testis lobes wer[e] present in the ovaries of the females of these species.

There is no evidence to show that these latter two species of *Triops* are ever any[-]thing but bisexual; in all the material I have examined of these species the larg[e] samples invariably contained both sexes, and there are no records in the literatur[e] of females occurring in large numbers without males. In *T. cancriformis* there appear[s] to be a complex situation: in the southern parts of its range bisexuality is norma[l] and a female from Algeria had no testis lobes; but in the more northerly region[s] males occur sporadically, often in very low proportions, so that some of the female[s]

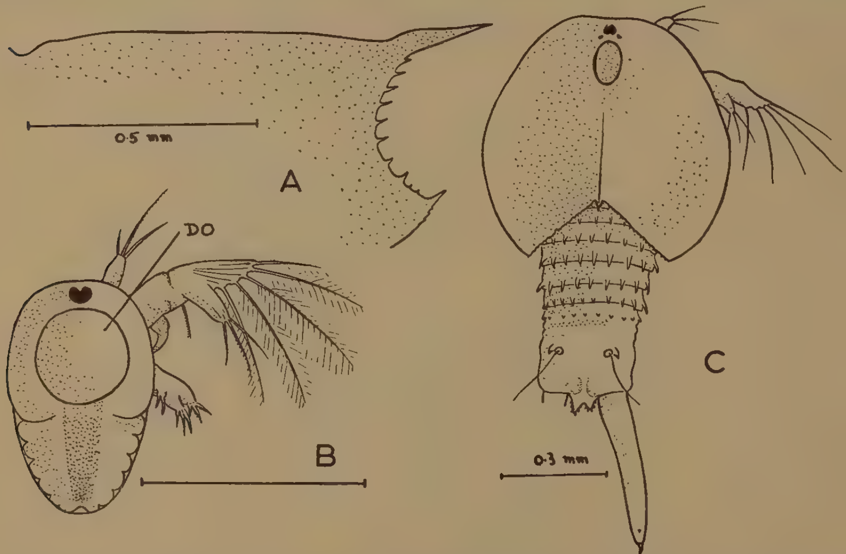

FIG. 13. Notostracan larvae. A = carina of instar 3 *Lepidurus apus*; B, metanauplius of *Triops cancriformis*; C, Neonatus of *Lepidurus arcticus*. (*do* = dorsal organ.)

probably reproduce without fertilization. In the extreme north of the rang[e] (Britain, Sweden) males are unknown and here females contain ovotestes. Unfor[-]tunately I have not been able to examine the gonads of females from a populatio[n] with sporadic male occurrence. Mathias (1937) gives a review of the occurrence[s] of males of this species.

In *Triops longicaudatus* the geographical distribution of males is not so clear[;] however, specimens from Californian rice fields where males are unknown containe[d] ovotestes, and Linder (1952) reports examining many specimens from the Galapago[s] Islands without finding males. Uéno (1935) records this species in Japan and foun[d] no males in 78 specimens. It may be that all the populations of this species from th[e] Pacific region are hermaphrodite, for the small samples that I have seen from Hawa[ii] (Oahu) and from New Caledonia contained no males.

Reproduction in *Lepidurus* is less well explored ; it is known (above) that herma-hrodite individuals occur in some species, but males of these are also known in some opulations although their geographical distribution is not clear. The three long odied species all appear to be bisexual.

The size of the egg in *Triops* is variable, being larger in long bodied forms irres-ective of species ; with this is correlated a size difference in the mature follicles in

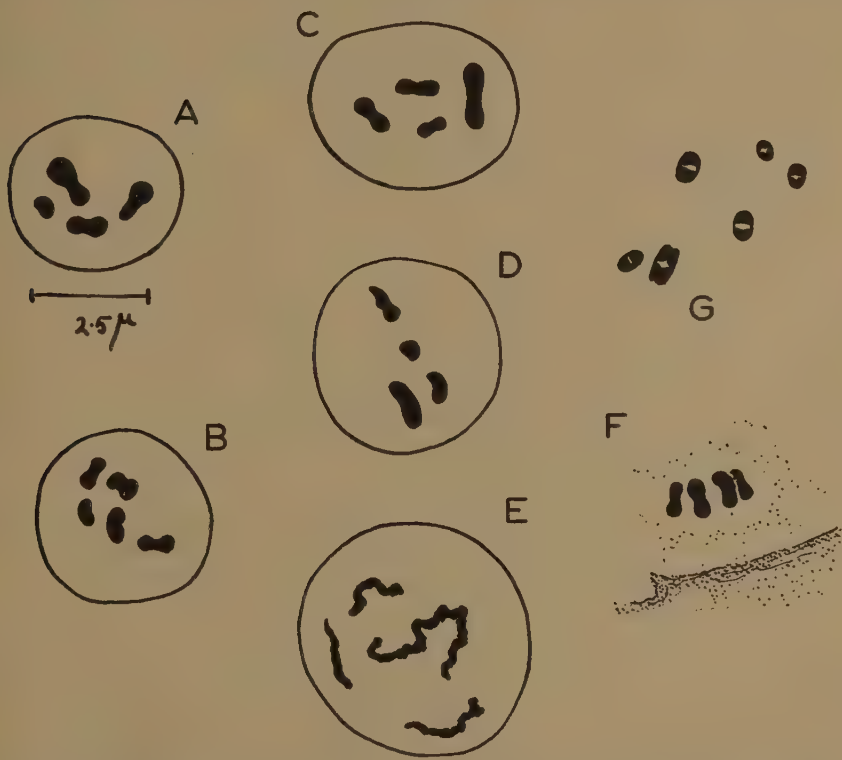

FIG. 14. Notostracan chromosomes. A–C, 2° spermatocyte telophase ; D–E, young oocyte ; F, resting unfertilized ovum ; G, spermatocyte diakinesis. A, *Triops longicaudatus* ; B, *T. australiensis* ; C, D, E, *T. granarius* ; F, *T. cancriformis* ; G, *Lepidurus apus*. (G is half the scale of the remainder and is redrawn from Goldschmidt, 1953.)

ıe ovary : *T. cancriformis* (33 segments), 0·28 mm. ; *T. granarius* (38 segments), ·45–0·52 mm. This size difference is correlated with size differences in the resultant ggs and larvae, the long bodied forms having the largest larvae. In *Lepidurus* the ifferences may be even more marked and are diagnostic of species in at least one ase ; the larvae of *L. arcticus* hatch at a later stage of development than those of ıe other species (Text-fig. 13), and the eggs are very much larger, the ovarian

follicles are relatively few in number, large and elongated in form, and completely fill the space above the gut.

CYTOLOGY

Moore (1893) was the first to examine the Notostraca cytologically, and from observations on the divisions of somatic cells he concluded that *Triops cancriformis* was amitotic ($2n = 1$).

While the present work was in progress, Goldschmidt (1953) recorded chromosomes in the testes of *Lepidurus* sp. from Palestine, finding that aceto-orcein squashes gave diakinesis stages where $n = 6$ (Text-fig. 14G). I have since determined her material as *L. apus lubbocki.*

Using testis smears I found that two populations of *Triops granarius* from South Africa showed the number $n = 4$; this was most clearly seen in the telophase stages of the spermatocyte (Text-fig. 14C). This number was confirmed in females of the same populations in which a haploid set of chromosomes was readily seen in the very early oocytes (Text-fig. 14D, E).

Sections of the ovotestes of *Triops cancriformis* from the European cultures showed $n = 4$ in the oocytes, most clearly in the late oocytes or ova, resting in the longitudinal oviduct (Text-fig. 14E); squashes of the same gonads showed $n = 4$ in secondary spermatocyte telophases in the testis lobes.

In both of the above species of *Triops* the diploid number, $2n = 8$, was confirmed by finding mitoses in cells of the expanding follicle walls, at the stage of increase in size of the oocyte and nutritive cells. In *T. longicaudatus* from California the number $n = 4$ was seen in early oocytes (Text-fig. 14A) and in spermatocyte telophases, but it was not possible to confirm the diploid number.

A single male of *Triops australiensis* from Kalgoorlie was available and testis smears were made from it which showed, in the spermatocyte telophase, a complement of $n = 5$; this number was counted in at least 16 nuclei. The 5 chromosomes

TABLE II.—*Chromosome numbers of Notostraca*

	Haploid number		Diploid number
	Males	Females	Females
L. apus lubbocki	6 (diakinesis)	—	—
T. c. cancriformis	4 (2° spermatocyte telophase)	4 (resting oocyte)	8 (follicle duct epithelium)
T. granarius	4 (2° spermatocyte telophase)	4 (young oocyte)	8 (follicle duct epithelium)
T. l. longicaudatus	4 (2° spermatocyte telophase)	4 (young oocyte)	—
T. a. australiensis	5 (2° spermatocyte telophase)	—	—

n this haploid set are all sub-equal in length (Text-fig. 14B), and it seems probable hat this situation could have arisen by the fragmentation of one chromosome in a et of four, such as the other species possess, in which one is nearly twice as long as he other three.

My findings and those of Goldschmidt are summarized in Table II, and both agree n ascribing a low number of chromosomes to the Notostraca so far examined. Ioore's account of amitosis may be true of the cells that he studied, but even hat is doubtful in view of my chromosome counts in epithelial cells; his inference f a single chromosome was obviously incorrect.

All the *Triops* material was fixed in Carnoy's or Susa's fluids and was stained with he Feulgen reaction.

BIOLOGY

Very many accounts of the ecology of the Notostraca and of their appearance in emporary pools have been published, and a clear picture of their biology can be erived from the literature.

There appear to be almost no ecological differences between the species of *Triops*, slight difference between *Triops* and most species of *Lepidurus*, and a marked ivergence between *L. arcticus* and the rest of the Notostraca.

So far as is known, *Triops* occurs only in waters which dry out regularly, and the ggs normally hatch in the field only after a period of dessication. The habitat self may vary a great deal in size from tiny rain pools and cart-ruts to large tempor- ry lakes (Main, 1953) and the water may be fresh as in the Hampshire locality Hobson and Omer-Cooper, 1935), brackish as in the Scottish pools (Balfour-Browne, 909), or saline as in the lakes on the Tibetan plateau (Schlagintweit, 1872) and in ustralia (Main, 1953).

The farming practice of rice fields makes these ideal situations for *Triops*, which re sometimes present in enormous numbers and have been recorded as a rice field est from many parts of the world (they uproot the rice seedlings).

Lepidurus may occur in temporary pools, but there seems to be a tendency for nost species to live in waters which dry out less regularly than the *Triops* pools. undblad (1920) records that *Lepidurus apus* is a spring form which appears when the emperature rises early in the year in ponds or ditches which have held water all the vinter; Linder (1952), on the other hand, says that he has seen the same species n Sweden in temporary pools. *L. apus viridis* occurs in a pool near Christchurch, New Zealand, which dries out in normal years, but is only very rarely found in neigh- ouring permanent ponds (G. Parry, personal communication). *Lepidurus* spp. egularly occur in temporary, often alkaline, pools in North America (J. Lynch, in tt.). L. Glauert has sent me a map showing all the records for *Triops* and *Lepidurus* n Western Australia and it is clear that *Lepidurus* is restricted to the south-western oastal belt where there is regular winter rain and *Triops* to the arid interior where ainfall is, at the most, sparse.

Lepidurus arcticus is confined to the boreal and alpine regions of the Holarctic, vhere it may occur in large lakes and form an important food of Salmonidae and vhere the eggs could never be dessicated (Sømme, 1934), it is also in pools which

normally do dry out each year (J. Mohr, in litt.). The only other records of *Lepidurus* occuring in lakes refer to *L. lynchi* (Linder, 1952).

It has been thought that there is a difference between the two genera in the conditions necessary for the hatching of the eggs: Fritsch (1866) and Grasser (1933) thought that *Triops* eggs could hatch only after dessication, while Brauer (1877) believed that the eggs of *Lepidurus* were incapable of withstanding dessication. Schaeffer (1756) and Kozubowsky (1857) showed that the eggs of *Triops* were sometimes capable of hatching without drying out. This has been confirmed in the present work and it is now known that the eggs of at least three species of *Triops* can hatch out, after an interval for development, in the water in which they were laid, or will remain viable if dried out and will hatch when replaced in water. This accounts for the report by Mathias (1937) that *Triops* has two types of eggs: the one drought resistant and the other not.

Fox (1949) reported that the eggs of *Lepidurus apus viridis* were able to hatch after drying, and I have confirmed this with another mud sample from the same locality as his; *L. arcticus* from Iceland were also hatched from dried eggs. The ecology of *Lepidurus* outlined above indicates that the eggs of this genus must in many cases be drought resistant.

The eggs of *Triops* probably do not often hatch out without prior dessication, as the water must have a low osmotic pressure for this to occur, a condition unlikely to be found on the bottom of a pool where the eggs are laid, but most likely when the pool refills with water after rain and the eggs float to the surface.

SYSTEMATICS

From the analysis of the characters used in the systematics of the Notostraca it is evident that many of the obvious differences between individuals must be correlated with differences in the number of body segments (Text-fig. 2); in *Triops* there is no discontinuity in the variation of this number, so that neither the number itself nor characters correlated with it can validly be used in the separation of species.

In this genus, as the number of segments increases to give a long bodied form so the carapace becomes smaller, rounder and flatter; the number of legs remains about the same and consequently the apodous number becomes higher; the furca, and the endites of the first thoracic appendage become relatively shorter; the dorsal organ becomes larger, less elevated, and more often triangular in outline; the sulcus spines become smaller and more numerous, and the terminal spine of the carina is more frequently absent; sexual dimorphism becomes more marked.

Similarly, certain characters are correlated with the sex of the specimen; males tend to have more segments than females and so the characters outlined in the previous paragraph vary from male to female within a population; characters other than these also show sexual dimorphism: the efferent duct of the shell gland is longer in males than in females; endites 5 and 6 of the second thoracic appendage are more nearly equal in length in females; the 11th thoracic appendage bears a brood pouch in females; the ventral armature of the furca of males is coarse, often forming scales rather than spines, and with this is correlated the ventral armature of the telson and apodous segments, which vary in the same way between males and females.

These two considerations then—segment number and sex—invalidate a number of haracters in the systematics of *Triops*. With those that remain there appear to e good grounds for dividing the genus into four groups, each with a geographical asis. The valid characters appear to be : the armature of the telson, the presence or bsence of the second maxilla, and the arrangement of the eyes and dorsal organ.)f these the most important is the armature of the telson, which is diagnostic for ach group ; the other characters, together with a few less well-marked ones, confirm his primary grouping.

Two groups are partially sympatric, and here there is no tendency to hybridize nd no intermediates have been found in the areas of overlap ; there is a record, noreover, of two species—which correspond to two of these groups—living in the ame pools in several localities in Morocco (Pérès, 1939). These two forms, therefore, ehave precisely as biological species (*sensu* Mayr, 1942) would be expected to do vhen they become sympatric ; it seems justifiable to consider them, therefore, as pecies and since the degree of morphological difference between all four groups is imilar to that found between these two, then all four may equally well be regarded s species.

Each species, then, has a geographical basis and a clear cut character in the telson rmature, but contains populations which are remarkably different in general appear-nce depending on the number of body segments in the specimens. What determines he body length is completely obscure, for there appears to be a general tendency or the longer bodied animals to occur in the warmer regions of a species range, but here are many blatant exceptions to this generality ; Barnard's *Apus ovamboensis* s a population of exceptionally short bodied *Triops granarius* from a very hot and ry part of Africa.

It is likely that an experimental study of the effect of environmental factors on norphology would throw some light on this problem, for perhaps the effects are seen nly after a considerable number of generations.

Several species show some indications of the presence of geographical races ; the ifferences between these are much slighter than the specific differences, and their istribution indicates that the geographical barriers between them are very slight. *'riops cancriformis* will serve as an example ; the populations in Morocco and outhern Spain differ in several respects from the rest of the species, even though n Spain there is no geographical barrier where the change occurs, and there is some vidence that intermediates occur where the races meet, for in Seville and near Gib-alter the specimens are identical with the Moroccan ones and from Valencia they are imilar to the specimens from the rest of Europe, but in Ciudad Real—midway etween the two areas—the specimens are intermediate. A similar zone of inter-nediates seems to occur in Spanish Morocco east of Ceuta.

Ghigi (1921) considered these races of *Triops cancriformis* to be species and des-ribed them as such ; Colosi (1922) and Pérès (1939) referred to Ghigi's species as 'arieties of the single species *T. cancriformis* but Gauthier (1934) used a true rinomial nomenclature and considered them to be sub-species or geographical races ; follow this nomenclature and believe them to be sub-species in the sense that Iuxley (1942) and Mayr (1942) used the term.

The arrangement of the species seems to follow different principles in *Lepidurus* from that in *Triops*, and the following account owes very much to the work of Linder (1952) who demonstrated the existence of two species-groups within the genus, each group characterized by its segment numbers.

The variation in segment number in *Lepidurus* is not so great as in *Triops*, and many characters show no correlation with this number in *Lepidurus* though the correlation is obvious in *Triops*: the armature of carina and sulcus; the endites of the first thoracic appendage; the number of apodous segments and the size and shape of the dorsal organ. The segment number shows a marked discontinuity at about 30; the vast majority of specimens have less than this number, and those which have more are aberrant in other respects.

Within the short bodied group there is relatively little differentiation, but *Lepidurus arcticus* can be separated at once, and is distinguished by its range, its habitat, its relatively short supra-anal plate and endites. The remainder of the group appears to comprise a single species, with a few rather ill-marked, but very widespread, sub-species.

Linder (1952) showed that *Lepidurus couesii* was conspecific with specimens determined as *L. macrourus* Lilljeborg. I can find no differences between the specimens that I have seen of either of these species and those of the European *L. apus*. The ranges of variation in the segment number are similar, the size and armature of the supra-anal plate is the same, and so is the armature of the carapace.

In California a form occurs which is admitted as a species by Linder, *Lepidurus packardi*; in these specimens there is usually a slightly higher number of segments than in the normal *L. couesii* (= *L. apus*), the apodous number tends to be higher, and the sulcus spines are very small, numerous and closely packed. In the Mediterranean region there occurs a form which diverges from typical *L. apus* in a similar way except that the sulcus spines are normal. Both of these forms replace the typical race over very restricted areas, but there appear to be no effective geographical barriers separating the several ranges from one another, and for these considerations I propose to consider these forms to be sub-species of the typical and widespread *L. apus*.

The Australasian forms do not differ from typical *Lepidurus apus* as much as do the above two sub-species, and many specimens would be indistinguishable if placed in a sample from Europe. However, I have seen no specimens which have the high number of central spines on the supra-anal plate which are very common in the typical *L. apus*, so that there is a slight degree of morphological differentiation and I propose to consider the Australasian form as another sub-species, *L. apus viridis*. The South American forms which I know only from descriptions must be considered as another sub-species of *L. apus*.

The rest of the genus comprises the few longer bodied specimens which are known. All have coarse and sparse marginal spines on the supra-anal plate—a character which they share with *Lepidurus arcticus*—and a low number of central spines on the same structure; specimens from three localities bear uniquely large spines on the carina and the carapace margin and these are Linder's *L. lynchi*, typical form and var. *echinatus*. A small sample from Russia has a considerably higher apodous

number than the rest of this group and shares with *L. lynchi* a peculiar arrangement of the eyes and the dorsal organ, which resembles the arrangement in *Triops australiensis* where the anterior margin of the dorsal organ may be placed well behind the posterior margin of the eyes. A single specimen from Utah was placed in this species-group by Linder on account of its segment number and seems to agree with the description of *Lepidurus bilobatus* Packard, having a normal carapace armature and normal arrangement of the eyes and dorsal organ. The only possible arrangement at the moment is to consider all these three forms as three separate species, but it seems very probable that future work will be able to find a connection at least between *L. bilobatus* and the Russian sample (*L. batesoni* sp. n.) and perhaps between these and *L. apus*.

It will be noted from the foregoing account how widespread are the species of the Notostraca and this is probably accounted for, as it is in some other invertebrates, by their passive distribution ; the dried viable eggs must be blown around by wind, and transport by birds is not unthinkable, for the eggs when laid are extremely sticky and remain so for some days while the shell hardens, and so could presumably adhere to larger animals, The eggs of other phyllopods are known to be capable of passing unharmed through the guts of amphibia (Mathias, 1937), and birds are known to eat Notostraca ; starlings (Decksbach, 1924) and gulls (Balfour-Browne, 1909) are recorded as feeding on *Triops cancriformis*, and Summerhayes and Elton (1923) watched Arctic terns feeding *Lepidurus arcticus* to their young, and thought that they might drop them accidentally into fresh pools on their way to the nest.

A passive distribution such as this must mean that geographical barriers are not nearly so effective as they are for sedentary, or non-passively distributed animals, and has produced species with world-wide distribution in other animals, such as Tardigrades and Rotifers.

In addition, the group has a very long geological record and has had ample time to occupy all suitable areas ; fossils from the Permian (Guthorl, 1934) are clearly Notostracan carapaces, and forms from the Triassic of Europe (Trusheim, 1938) are certainly *Triops* and differ from extant *T. cancriformis* only in the small size of the terminal carinal spine. The upper Triassic *L. stormbergensis* (Barnard, 1929) from South Africa is very similar to recent species except that the supra-anal plate has, apparently, no central spines as in some extant *L. arcticus*.

It is impossible from these few fossils to give any account of the history of the group, except to point out how little evolution has occurred in the space of 170 million years since the Triassic forms were alive.

However, something can be deduced about more recent changes in distribution. During the Pleistocene glaciations *Lepidurus arcticus* was much more widespread in western Europe than it is now ; this species is known from lacustrine beds of that time from Scotland (Bennie, 1894) and from the Isle of Man (Geikie, 1894), and now shows in Scandinavia the typical distribution of a boreo-alpine relict occurring at sea level in the North and at progressively greater altitudes towards the South (Sømme, 1934).

Triops cancriformis must have been absent from much of its present range at the same period, and the post-glacial extension may have been performed largely by

hermaphrodites, which predominate in the northern parts of its range; for these would be more efficient in dispersal as only a single egg would be required to effect a colonization. Perhaps the increasingly sporadic occurrence of males towards the north indicates a spread northwards of bisexuality.

All the known rice field populations consist entirely of females (or hermaphrodites if parthenogenesis is assumed not to exist in these animals) and this strengthens the above argument, for these are relatively new habitats for Notostraca, and a colonization by hermaphrodites ahead of the bisexuals seems to have occurred.

The westward extension of *Triops longicaudatus* across the Pacific from the largest area of distribution in North America, may also be of relatively recent origin and has apparently been performed again by hermaphrodites, for no males are known from the Pacific populations (p. 47).

Nomenclature

Keilhack (1909) and Fox (1949) have shown that the generic name *Apus* Schaeffer, 1756 should be rejected in favour of *Triops* Schrank, 1803; this practice will both accord strictly with the Rules of Nomenclature and will avoid further confusion in this genus, and in the avian genus *Apus* Scopoli, 1777. I therefore propose to follow Keilhack in the use of *Triops*.

The use of trinomials is necessary to describe formally the geographical sub-species recognized.

The lists of synonymies before each species are not complete lists of references to that species, for these would be too long and not very useful—but include (*a*) the names, and the various spellings of each name, that have been applied to that species, and (*b*) important descriptive works.

Apus has been applied to Crustacea other than Notostraca; *Apus pisciformis* Schaeffer is an Anostracan and *Apus caudatus* De Kay, was a crustacean parasitic on a crab.

Identification

The following key should serve to identify specimens down to species, but the user must bear in mind the extent of variation in any character and not expect the figures to match the specimen in details of armature. It would be very valuable if the segment number, the apodous number, and the number of appendages were given in any future records.

It must also be remembered that every individual in a sub-species may not be typical of it; many ornithologists consider a sub-species to be valid if 75% of its specimens can be placed in it without question. In *Triops cancriformis*, for example, it may be difficult to ascribe single specimens to the nominate race or to *T. cancriformis simplex*, for the smooth carina which is typical of the latter occurs in some individuals of the former, but I have no knowledge of whole samples of the nominate race with smooth carinas.

Key to species of Notostraca

1. Supra-anal plate present (Text-fig. 7) . . . . (*Lepidurus*) 2.
   Supra-anal plate absent . . . . (*Triops*) 6.

Segments more than 30 . . . . 3.
Segments less than 30 . . . . 5.
Anterior margin of dorsal organ between eye tubercles (Text-fig. 4E) *L. bilobatus* (p. 53).
Anterior margin of dorsal organ well posterior to eye tubercles (Text-fig. 4D) . . 4.
Carina and/or lateral margins of carapace with large spines. (Text-fig. 3) Apodous segments 3–5 . . . . *L. lynchi* (p. 53).
Without large spines on carina or lateral margin. Endite 6 of first thoracic appendage as in Text-fig. 10D. Apodous segments 8–9 . . . . *L. batesoni* (p. 54).
Supra-anal plate short, 0–5 spines centrally, marginals few (Text-fig. 7C). Endites scarcely project beyond edge of the carapace . . . . . *L. arcticus* p. 52).
Supra-anal plate long (Text-fig. 7A, B), 4–100 central spines, marginals numerous. Longest endites with 3/4 of their length projecting beyond edge of carapace (Text-fig. 2*i*) . . . . *L. apus* (p. 50).
Second maxilla absent . . . . 7.
Second maxilla present (Text-fig. 11) . . . . 8.
Posterior marginals sub-equal to medians and well forward of the margin (Text-fig. 5D$_2$). Medians large, 1–4 in number, in a row . . . *T. longicaudatus* (p. 46).
Posterior marginals reduced and marginal. Medians small, scattered when more than 3–4, often absent. (Text-fig. 6B) . . . . . *T. australiensis* (p. 48).
No supernumerary spines on the apodous segments (Text-fig. 8A). Medians large, 1–4, in a row (Text-fig. 5B$_2$) . . . . *T. cancriformis* (p. 41.)
Supernumerary spines present on apodous segments (Text-fig. 8B). Medians of various sizes, scattered except when less than about 5 are present, when they form an irregular row (Text-figs. 5C$_2$, 6A, A$_1$) . . . . . *T. granarius* (p. 44.)

Genus *TRIOPS* Schrank, 1803

756. *Apus* Schaeffer (in part).
758. *Monoculus* Linn. (in part).
303. *Triops* Schrank.
921. *Thriops* (sic.) Ghigi.
921. *Proterothriops* Ghigi.

Triops is at once separable from *Lepidurus* by its lack of a supra-anal plate ; even a structure resembling a rudimentary plate (Text-fig. 7C) is found in some specimens f *Triops cancriformis* (Linder, 1952) there is never any doubt as to which genus a pecimen belongs.

Proterothriops was erected by Ghigi for the reception of the long bodied forms of ne genus ; he was struck by the great difference in general appearance between ong and short bodied forms which I have now been able to show to be conspecific n a number of cases.

Binoculus Geoffroy, 1762 and *Apodis* Zaddach, 1841, are not in a strict binomial ystem and are ignored on this account.

Triopes Schrank, 1803, appears later in the publication than *Triops* and must be egarded as a spelling lapse.

TRIOPS CANCRIFORMIS (Bosc)

756. *Apus cancriformis* Schaeffer (in part).
758. *Monoculus apus* Linn. (in part).
301. *Apus cancriformis* Bosc.

1801. *Apus viridis* Bosc.
1803. *Triops palustris* Schrank.
1816. *Apus montagui* Leach.
1871. *Apus himalayensis* Packard.
1885. *Apus halicienis* Fiszera.
1885. *Apus lublinensis* Fiszera.
1885. *Apus varsovianus* Fiszera.
1909. *Triops cancriformis* (Bosc) Keilhack.
1909. *Apus cancriformis bidens* Sidorov.
1909. *Apus cancriformis transcaucasicus* Sidorov.
1921. *Thriops simplex* Ghigi.
1921. *Thriops mauretanicus* Ghigi.
1921. *Thriops apulius* Ghigi.
1922. *Thriops cancriformis* var *simplex*, Colosi.
1953. *Triops cancriformis simplex* (Ghigi, 1921) Margalef.
1953. *Triops cancriformis mauretanicus* (Ghigi, 1921) Margalef.

TYPE. Original is unknown, and designation of neotypes desirable. A sample from Kirkudbrightshire is selected (BMNH, 1907.10.17.1–4) and consists of a number of neoparatypes.

RANGE. Western Europe (Spain to Sweden) east to Russia; North Africa, Balkans, Asia Minor, Middle East to India. Individual records too numerous to list; Lundblad (1920) gives many for Europe, Decksbach (1924) many for Asia. Does not extend beyond 60° N and range in Russia obscure, but no records authenticated for Eastern Asia.

HABITAT. Temporary fresh or brackish waters; occurrence depends on the pools filling when the temperature is high enough for development, so usually summer form in Europe, spring form in N. Africa.

Rice field pest in N. Italy, Spain and La Carmargue.

DESCRIPTION. *Head.*—Dorsal organ round, oval or rarely triangular, small and with its anterior margin between the eyes. Second maxilla present in all specimens examined and relatively larger than in the rest of the genus.

Carapace.—Shape generally oval, more round in males. Carina with terminal equal to, or longer than, sulcus spines (Text-fig. 15); sometimes number of smaller spines on posterior carina. Sulcus spines long, 24–44, usually about 30.

Body.—Segments 32–35 in both sexes; apodous 4–7 in ♀♀, 5–9 in ♂♂. Apodous segments without supernumerary spines on ventral surface.

Telson.—Median spines large, 1–4, in a single median row (Text-fig. 5B). Furcal spines large, number sometimes varying from side to side of a single animal, and with few scattered spines on lateral face of telson anteriorly.

Posterior marginals small, fine and marginal in the adult, and posterior margin of telson sometimes drawn out to resemble a rudimentary supra-anal plate (Text-fig. 6C).

Furca generally long.

Appendages.—48–57 pairs recorded, but variation probably greater. Endites of first thoracic appendage long.

Sexual dimorphism.—Not as well marked as in other species; no males with furcal scales seen. Abonyi (1926) records two sets of males in one summer in the same pool

of which the second batch had very reduced sexual dimorphism—so a dimorphism of males may exist ?

Larvae.—Metanauplius (Text-fig. 13); dorsal organ of instar 1 generally round.

Reproduction.—Bisexual and hermaphrodite; in the northern regions no males occur and such females as have been examined are hermaphrodite. In the South populations are bisexual and in central Europe males occur sporadically. Mathias (1937) reviews occurrence of males.

Geographical Races

1. *Triops cancriformis cancriformis* (Bosc)

Range. Whole of species range with exception of that occupied by the other two sub-species.

Description. Carina bears 0–10, generally 2–3, small teeth in front of the terminal spine (Text-fig. 15E) and no large samples without specimens showing these spines are known. Furcal spines small (Text-fig. $5B_2$). Dorsal organ round-oval.

Hermaphrodite and bisexual. Chromosome number $2n = 8$.

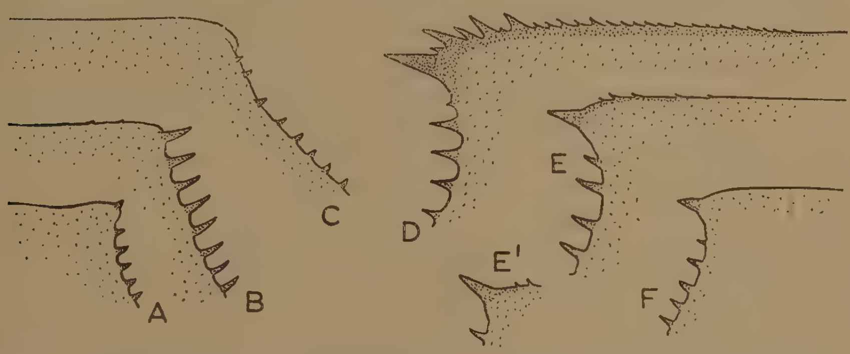

Fig. 15. Carinas of *Triops*. A–C, *T. granarius*; D, *T. cancriformis mauretanicus*; E, E_1, *T. c. cancriformis*; F, *T. cancriformis simplex*.

2. *Triops cancriformis simplex* Ghigi

Range. North Africa, Ceuta to Egypt.

Description. Characters of *Thriops simplex* Ghigi. Carina quite smooth in front of the terminal spine (Text-fig. 15F); this is invariable in the specimens I have seen from this area, and in those seen by Gauthier (1934), Colosi (1922) and Ghigi (1921). Furcal spines small (Text-fig. $5B_2$). These populations frequently show a tendency to a general weakness in the strength of the armature and include the sample from Kebili (p. 14) which has specimens with no carapace armature whatever. The terminal spine of the carina is frequently reduced.

Apodous segments frequently higher in number than the nominate race (♀♀ 5–7, instead of 4–6).

Bisexual.

3. *Triops cancriformis mauretanicus*, Ghigi

Range. N.W. Africa: French Morocco and Tangier. S. Spain and Balearics (Minorca).

Description. With the characters of *Thriops mauretanicus* Ghigi: armature very strongly developed; carina with a number of teeth posteriorly (Text-fig. 15D), the largest often sub-equal to the terminal spine. Furcal spines very large (Text-fig. 6C); ventral marginal spines on apodous segments very coarse. Apodous number is similar to that of sub-species 2. Dorsal organ oval.

Bisexual.

Synonyms

Apus viridis Bosc was applied to figures of Schaeffer (1756) which showed juvenile *Triops cancriformis; Triops palustris* Schrank is presumably of this species because of its N. European locality; *Apus montagui* Leach, type in BMNH and clearly of this species; *Apus himalayensis* Packard, author's figures show clearly the *cancriformis*-type telson; *Apus varsovianus*, etc. Fiszera, figures similarly show *cancriformis*-type telson; Sidorov's two sub-species are insufficiently described and can both be referred to this species; *Thriops apulius* Ghigi; this could be either sub-species 1 or 2 as it was a single specimen with a smooth carina, but from its Italian locality is probably of sub-species 1.

TRIOPS GRANARIUS (Lucas)

1864. *Apus granarius* Lucas.
1865. *Apus numidicus* Grube.
1877. ? *Apus dispar* Brauer.
1877. *Apus sudanicus* Brauer.
1880. *Apus dukeanus* Day.
1886. *Apus bottegoi* Prato.
1886. *Apus namaquensis* Richters.
1893. *Apus sudanicus* var. *chinensis* Braem.
1893. ? *Apus sudanicus* var. *braueri* Braem.
1893. *Apus numidicus* var. *strauchii* Braem.
1893. *Apus numidicus* var. *dybowskii*, Braem.
1895. *Apus somalicus* Wedenissow.
1899. *Apus bottegoi*, Bouvier.
1899. *Apus trachyaspis* Sars.
1899. *Apus sculleyi* Sars.
1899. *Apus namaquensis* Sars.
1899. *Apus granarius* Sars.
1907. *Apus elongatus* (nom. nov. for *namaquensis* Sars) Thiele.
1920. *Apus zanoni* Colosi.
1921. *Apus asiaticus* (nom. nov. for *granarius* Sars) Gurney.

1922. *Triops uebensis* (nom. nov. for *bottegoi* Bouvier) Colosi.
1924. *Apus ovamboensis* Barnard.
1927. *Apus numidicus* var. *sinensis* Uéno.
1929. *Apus cancriformis*, Barnard. (non Schaeffer, 1756).
1929. *Apus sudanicus*, Barnard. (? Brauer, 1877.)
1934*a*. *Apus granarius*, Gauthier.
1937. *Apus sudanicus*, Gauthier. (non Brauer 1877).
1939. *Apus numidicus*, Pérès.
1940. *Apus sinensis* Uéno.
1952. *Apus mavliensis* Tiwari.
1952. *Apus orientalis* Tiwari.

TYPE. MNHNP ; ♂ Holotype, unregistered other than label " Type *A. granarius* Lucas ".

RANGE. South Africa to China ; the whole of Africa except for unsuitable forest regions in west and centre ; Middle East, India, central and eastern Asia to the north Chinese coast. Single sample in MNHNP labelled " near Paris " almost certainly mistake in labelling.

HABITAT. Temporary fresh and brackish waters ; unknown from rice fields ; Pérès (1939) compares its distribution in North Africa with that of *Triops cancriformis* and finds latter in steppe zones (300 mm. annual rain) and in the sub-steppe (300–500 mm.) while present species is restricted to the sub-steppe.

DESCRIPTION. Shows great variation in body length and includes very short and long bodied forms with all the associated variation.

Head.—Dorsal organ triangular, oval or round in the short bodied forms, anterior margin between the eyes. Second maxilla present in all specimens examined except in one case (see below).

Carapace.—Shape variable, round to oval. Carina with terminal spine in short bodied forms only (Text-fig. 15), generally smooth. Sulcus round (or squared in some African short bodied forms), spines many, often reduced in size, 24–72.

Body.—Segments : ♀♀, 32–42 ; ♂♂, 32–43. Apodous : ♀♀ 4–13 ; ♂♂, 6–14. Apodous always with varying number of supernumerary spines ventrally (Text-fig. 8B).

Telson.—(Text-fig. $5C_2$, 6A). Medians small, numerous, scattered, but when low in number may form a rough row medianly, though this never as accurate as in *Triops cancriformis*, and spines smaller. Furcals small and with many scattered in front of them. Posterior marginals small, squat and marginal. Furca variable with body length.

Appendages.—44–46 recorded, but variation probably much greater than this. Endites of first thoracic appendage variable with body length (Text-fig. 2).

Sexual dimorphism.—Strong in many long bodied specimens, males having strong scales on furcal (Text-fig. 8D).

Larvae.—Metanauplius, those seen having in instar 1 a trapezoid-shaped dorsal organ which later changes to triangular.

Reproduction.—Bisexual. Chromosome number $2n = 8$.

Geographical Races

With present knowledge not possible to recognize any with certainty. Some indications known—many South African (not S.W.A.) and Middle East (Bombay-Baghdad) specimens have reduced sexual dimorphism even in long bodied forms; these correspond to *Apus asiaticus* Gurney and this name may eventually be applied to a race with a restricted range. Some specimens from Eastern Asia have reduced second maxilla, and this is even absent in few out of large sample (BMNH 1935. 6.18. 7–12) and these might be separated off as another race, but evidence too weak at present.

Synonyms

Apus sudanicus Brauer belongs here doubtfully as the description is inadequate and I have not seen the types, but Barnard's specimens determined as this are certainly *Triops granarius*. A number of species are placed here on evidence of original descriptions: *A. numidicus* Grube, Braem's varieties of *A. numidicus* and *A. sudanicus* (exc. var. *braueri* which is doubtfully here for it refers to Brauer's description of *A. sudanicus*), *A. somalicus* Wedenissow, Sars' three species (1899), *A. granarius* Sars and the nom. nov. *asiaticus* Gurney, Uéno's var. *sinensis* and *A. sinensis*. I have seen the types of *A. granarius* Lucas, *A. bottegoi*, Bouvier, *Apus ovamboensis* (= *cancriformis* sens Barnard), and of Tiwari's two species. *A. mavliensis* Tiwari, in spite of its odd appearance is clearly only a young form of this species. *A. bottegoi* Prato is insufficiently described and may belong here or to the previous species.

TRIOPS LONGICAUDATUS (LeConte)

1846. *Apus longicaudatus* LeConte.
1852. *Apus domingensis* Baird.
1871. *Apus aequalis* Packard.
1871. *Apus lucasanus* Packard.
1871. *Apus newberryi* Packard.
1907. *Apus frenzeli* Thiele.
1916. *Lepidurus patagonicus*, Bruch. (non Berg, 1900).
1944. *Triops pampaneus* Ringuelet.
1947. *Apus biggsi* Rosenberg.
1947. *Apus oryzaphagus* Rosenberg.
1952. *Apus longicaudatus*, Linder.

Range. Western North America, south of 50° N, through Central to South America, where only very scattered records (Thiele, 1907; Bruch, 1916; Ringuelet, 1944; Linder, 1952). W. Indies, Galapagos Islands, Hawaii, Japan and New Caledonia.

Habitat. Temporary fresh waters, rice fields in California and Japan.

Description. As variable as the preceding species, but not so many short bodied forms seen.

Head.—Dorsal organ usually triangular, round in short bodied forms, and anterior margin between the eyes. Second maxilla absent in all the specimens seen.

Carapace.—Text-fig. 2G., H). Shape varies from oval to round with segment number. Terminal spine of carina very small when present, but generally absent. Carina finely denticulate along whole length in some specimens. Sulcus tends to be broad and shallow, spines variable in size, 24–60.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 35–44. Apodous segments : ♀♀, 5–12 ; ♂♂, 10–13 in material examined. Apodous segments with varying number of supernumerary spines on ventral surface.

Telson.—(Text-fig. 5 D_2.) Medians large, 1–3, in a single row in the midline. Furcal spines smaller than those of *T. cancriformis*. Posterior marginals very large, set in the adult well forward of the margin, often pointing vertically. This arrangement of marginals unique and all specimens of this species have it.

Appendages.—54–66. (Linder's data mainly) : endites of first thoracic appendage variable with segment number.

Sexual dimorphism.—Well marked in specimens with high segment numbers, males then having furcal scales.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius*.

Reproduction.—Bisexual and hermaphrodite, the latter only in California and Pacific region populations.

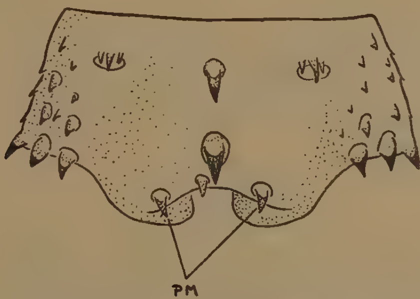

FIG. 16. Telson of *Triops longicaudatus intermedius*. (*pm* = posterior marginals).

GEOGRAPHICAL RACES

1. *Triops longicaudatus longicaudatus* (LeConte)

RANGE. That of species with exception of New Caledonia.

DESCRIPTION. With the characters described above. There may be a difference in the shape of the posterior margin of the telson on the forms from Galapagos and Hawaii as against continental American forms ; in the former the posterior margin is quite straight with no trace of an emargination in many specimens. This may well be evidence for a sub-species inhabiting these islands. Chromosome number $2n = 8$.

2. *Triops longicaudatus intermedius* subsp. n.

RANGE. New Caledonia. Two samples in MNHNP labelled " 93–1887 " and

" coll. Simon 25–96 " respectively are of this form and no others from the island are known to me. These specimens, all females, form the paratypes of the new subspecies. The name suggests that in their telson armature they are intermediate in form between their nominate race and the rest of the genus.

DESCRIPTION. Second maxilla absent, segments 39, apodous 8–9. Dorsal organ small, triangular to round. Carapace oval, terminal spine of carina very reduced, sulcus spines long, 24–30. Few supernumerary spines on apodous segments ventrally. Telson : medians large, 2–3, in mid-line, posterior marginals much smaller than in nominate race but well forward of the margin (Text-fig. 16). This is the most characteristic feature.

SYNONYMS

Apus obtusus James, 1823 and *Apus guildingi* Thompson, 1834 are clearly of this species on geographical grounds, but neither description is detailed enough to confirm this. Linder has shown that Packard's and Rosenberg's species are synonyms of this species. The diagrams of *A. frenzeli* and *Triops pampaneus* both show the *longicaudatus*-type telson, and Bruch's record of *Lepidurus patagonicus* is accompanied by a figure which certainly shows a *Triops*, and probably *T. longicaudatus*, though the telson is not very clear.

TRIOPS AUSTRALIENSIS (Spencer and Hall)

1896. *Apus australiensis* Spencer and Hall.
1905. *Apus sakalavus* Nobili.
1907. *Apus madagassicus* Thiele.
1911. *Triops gracilis* Wolf.
1911. *Triops strenuus* Wolf.

RANGE. The drier regions of Australia, where it may be locally very common. Madagascar.

HABITAT. Temporary fresh water, sometimes (Wolf, 1911 ; Main, 1953) in saline or alkaline pools and lakes.

DESCRIPTION. Includes extremes of long and short bodied forms ; from Australia several samples have been seen with aberrations (not damage) to limbs and lobes of limbs ; both females in a sample from Ayer's Rock have reduced 11th thoracic appendages so that these are but a stump with a duct running through it on one side of each specimen. Several samples from W. Australia have endites 5 and 6 reduced to rudiments on one side of the thoracic series.

Head.—Dorsal organ triangular, ovoid or " wide ", often set with the anterior margin well behind the eyes (Text-fig. 4B). Second maxilla absent in all specimens seen.

Carapace.—Shape variable, terminal carinal spine usually absent and carina frequently denticulate along the whole length. Sulcus round, often small, spines variable in size, and numerous, 28–62.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 36–44. Apodous : ♀♀, 5–12 ; ♂♂, 9–13. Apodous segments with varying number of supernumerary spines ventrally.

Telson.—Medians small, scattered, fewer than in *T. granarius*, often very few or even absent (Text-fig. 6B); furcal spines small, posterior marginals small, squat and marginal in the adult. Furca varies with the segment number.

Appendages.—48–66, but only few specimens counted. Endites variable with segment number.

Sexual dimorphism.—As in previous two species.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius.*

Reproduction.—Bisexual.

Geographical Races

1. ***Triops australiensis australiensis*** (Spencer and Hall)

Range. Continental Australia.

Description. With the characters described above. Chromosome number $2n = 10$.

2. ***Triops australiensis sakalavus*** (Nobili)

Range. Madagascar.

Description. Very similar to the nominate race, but median spines are rather more numerous in the specimens I have seen in MNHNP, which otherwise are clearly of this species, and not of *T. granarius*; the specimens have no second maxillae, the carinae are denticulate, and the median spines are relatively sparse compared with *T. granarius*.

Synonyms

Wolf's species are clearly *Triops australiensis*, showing the typical telson pattern and Main has already (1953) suggested uniting them with it. *T. madagassicus* and *T. sakalavus* are placed here on the assumption that only one species will occur in Madagascar, since sympatric species are the exception in the Notostraca, but future work will be needed to confirm this arrangement.

Genus ***LEPIDURUS*** Leach

1756. *Apus* Schaeffer (in part).
1758. *Monoculus* Linn. (in part).
1819. *Lepidurus* Leach.
1924. *Bilobus* Sidorov.

Distinguished at once from *Triops* by the presence of a supra-anal plate. In general, also, the segment number is lower, the carapace is longer and more compressed laterally, the sexual dimorphism is weaker than in the other genus.

Bilobus Sidorov was erected on the erroneous assumption that median incision of the posterior margin of the supra-anal plate was important systematically (see p. 22, and Linder, 1952).

LEPIDURUS APUS (Linn.)

1756. *Apus cancriformis* Schaeffer (in part).
1758. *Monoculus apus* Linn. (in part).
1801. *Apus productus* Bosc.
1819. *Lepidurus productus* Leach.
1850. *Lepidurus viridis* Baird.
1866. *Lepidurus angasi* Baird.
1873. *Lepidurus lubbocki* Brauer.
1875. *Lepidurus couessii* Packard.
1877. *Lepidurus macrourus* Lilljeborg.
1879. *Lepidurus viridulus* Tate.
1879. *Lepidurus kirki* Thompson.
1879. *Lepidurus compressus* Thompson.
1886. *Lepidurus packardi* Simon.
1893. *Apus extensus* Braem.
1900. *Lepidurus patagonicus* Berg.
1909. *Lepidurus apus* Keilhack.
1911. *Lepidurus hatcheri* Ortmann.
1921. *Lepidurus barcaeus* Ghigi.
1952. *Lepidurus couessii*, Linder.

RANGE. Europe (excluding Britain), North Africa, Palestine, Asia Minor, Russia ; North and South America ; New Zealand and Australia.

HABITAT. Temporary fresh waters, but perhaps less restricted to those which regularly dry out than, for instance, *Triops cancriformis*. Occurs in alkaline pools in North America.

DESCRIPTION. This species has the largest range of any known Notostracan and shows very little variation over the whole area.

Head.—Dorsal organ round or oval (Text-fig. 4E, F), anterior margin between the eyes with the possible exception of the specimens seen by Ortmann (1911) from Patagonia. Second maxilla present in all the specimens seen by me.

Carapace.—Oval, fairly compressed laterally but not so markedly as in next species. Terminal spine of carina only rarely absent. Sulcus spines usually long, rarely (*packardi*) reduced. Normally 35–50 in number.

Body.—Segments, 26–29 ; Apodous, 4–6. No supernumerary spines on apodous segments.

Telson.—Supra-anal plate relatively longer than in next species, the ratio carapace/supra-anal plate being about 4–6 in adults. The marginal spines of the plate are small and numerous in all except the South American forms. Central spines 4–100 or more, the higher numbers being borne on a distinct keel (Text-fig. 7A).

Appendages.—35–48 ; endites of first thoracic appendages reach to the end of the carapace in some, in others little longer than *L. arcticus*.

Sexual dimorphism.—Males occur, and the supra-anal plate is longer and more spatulate in these ; otherwise the dimorphism is weak.

Larvae.—Metanauplius in the European and New Zealand forms and probably in all. May differ from that of Triops by presence of rudiments of paired eyes in the first instar (Bernard, 1892 : 158).

Reproduction.—Bisexual and hermaphrodite.

Geographical Races

1. *Lepidurus apus apus* (Linn.)

Range. Europe (exc. range of next ssp.), Asia, North America (exc. California).

Description. Segments, 26–28; apodous, 4–5; supra-anal plate with 20–100 spines generally borne on a keel; marginal spines of plate fine and numerous. Bisexual and hermaphrodite.

2. *Lepidurus apus lubbocki* Brauer

Range. N. Africa, Palestine, Syria, Italy, Sicily.

Description. Segments, 27–29; apodous, 5–6; supra-anal plate (Text-fig. 7B) with fewer central and marginal spines than above ssp (3–20 centrals) and keel less prominent. Specimens from eastern part of the range tend to have the fewest central spines; endites relatively longer than nominate race. Bisexual. Chromosome number, $2n = 12$ (Goldschmidt).

3. *Lepidurus apus packardi* Simon

Range. California.

Description. Segments and supra-anal plate similar to sub-species 2. Sulcus differs from that of all other forms by having very many small spines forming a granulated margin. Bisexual.

4. *Lepidurus apus patagonicus* Berg

Range. South America (Chubut Territory, Patagonia).

Description. Segments, 29; apodous, 5. Marginal spines of supra-anal plate coarser and fewer than previous forms, central spines few. Sulcus spines as typical race. Bisexual.

5. *Lepidurus apus viridis* Baird

Range. New Zealand, Tasmania, and coastal or better watered regions of Australia.

Description.—Very similar to nominate race. Segments, 27–28; apodous, 4–5. Generally with low number of central spines on the plate (5–10), but one specimen from Tasmania had more than 20; average is much lower than in nominate race, however. I have seen no males.

Synonyms

I have examined the following types, and am satisfied that they are correctly placed here: *L. packardi*, *L. extensus*, *L. barcaeus*, *L. angasi*, *L. compressus*, *L. kirki*, *L. viridulus*. The rest are included on the basis of the original descriptions or on material previously determined.

Lepidurus lemmoni (Holmes, 1894). Holmes' description does not enable determination of his specimens with any here recognized, yet contains nothing to indicate

good differences from them ; the types are lost (Linder, 1952), and therefore it is advisable to abandon the species.

LEPIDURUS ARCTICUS (Pallas)

1793. *Monoculus arcticus* Pallas.
1883. *Lepidurus glacialis* Packard.
1892. *Lepidurus spitzbergensis* Bernard.
1893. *Apus productus* var. *glacialis* Braem.
1896. *Lepidurus glacialis*, Sars.
1927. *Lepidurus ussuriensis* Sidorov.

RANGE. Circum-polar Arctic regions ; Aleutians, North America ; Alaska to Labrador, Greenland, Iceland, Bear Island, Spitzbergen, Northern Palaearctic ; Scandinavia to Siberia.

HABITAT. Temporary fresh-water pools, the streams connecting pool systems, and large lakes which are permanent. A reservoir in the Norwegian mountains (Sømme, 1934).

DESCRIPTION. *Head*.—Dorsal organ oval, sometimes very elongated, anterior margin just between the eyes (Text-fig. 4G). Second maxilla present.

Carapace.—Oval, laterally very compressed. Terminal carina spine present, long. Rest of carina smooth.

Body.—Segments, 26–28 ; apodous, 4–5. Apodous without supernumerary spines on ventral surface.

Appendages.—41–46, but variation probably greater. Endites of the first thoracic appendage very short, scarcely reaching beyond margin of carapace (Text-fig. 10A).

Telson.—Supra-anal plate very small ; carapace/plate = about 12 in adults of 20 mm. carapace length. Median spines very sparse (0–5) and marginals few and coarse (Text-fig. 7C).

Sexual dimorphism.—Males rare, but known to have longer and more spatulate supra-anal plates.

Larvae.—Post-metanauplius (Poulsen, 1940, and my cultures), equivalent to about instar 3 of *Triops* larvae (Text-fig. 13).

Reproduction.—Bisexual and hermaphrodite. Males known from Bear Island in very low proportion of the population. (Sømme, 1934).

GEOGRAPHICAL RACES

None could be recognized in the material available, nor could Linder (1952) find any subdivisions of his material. *Lepidurus ussuriensis* Sidorov appears to be of this species, for the endites are shorter than is usual in other species, and the supra-anal plate is small (carapace/plate = about 9) and typical of this species in its armature. However, the endites are projecting more beyond the carapace than is usual in *L. arcticus* and may indicate a difference between this East Siberian form and the typical Arctic forms. The weakness of the carina and the elongate form of the dorsal organ confirm the placing of this species in *L. arcticus*.

LEPIDURUS BILOBATUS Packard

1883. *Lepidurus bilobatus* Packard.
1952. *Lepidurus bilobatus*, Linder.

RANGE. North America ; Utah, Colorado, probably Arizona (Linder, 1952).

HABITAT. Not known, but occurs in arid areas so presumably in temporary pools and lakes.

DESCRIPTION. Known only from Packard's description, and two further specimens ascribed to the species by Linder.

Head.—Dorsal organ round or oval, anterior margin set between the eyes.

Carapace.—Arrangement of sulcus spines normal.

Body.—Segments, 33 ; apodous, 6.

Telson.—Supra-anal plate with numerous small marginals, 4–6 centrals.

Appendages.—60 ; endites of first thoracic appendage as in *Lepidurus apus.*

Sexual dimorphism.—Males unknown.

Larvae, Reproduction.—Unknown.

LEPIDURUS LYNCHI Linder

1952. *Lepidurus lynchi* Linder.
1952. *Lepidurus lynchi* var. *echinatus* Linder.

TYPES. Holotype (♀) and allotype (♂) in Uppsala Museum ; paratypes USNM 82101 ; var. *echinatus.* Holotype (♀) USNM 82068, allotype (♂) USNM 82069.

RANGE. North America ; Washington, Nevada, and Oregon.

HABITAT. Apparently in lakes (Linder, 1952 . . . North end of Goose Lake in water two feet deep, muddy), but probably also in temporary pools.

DESCRIPTION. Long bodied form with unique carapace armature.

Head.—Dorsal organ round with the anterior margin set well behind the eye tubercles.

Carapace (Text-fig. 3).—Oval. Carina absent except when it bears series of unusually large spines. Specimens from first two localities have 0–20 of these carinal spines. Some of those from Oregon have series of large spines along posterior part of lateral margin in addition to carinal spines and carapace shape may be more round in these. But no useful purpose is served by the formal term var. *echinatus* for these latter forms ; *L. lynchi* is obviously characterized by the possession of large spines on carina and margin and there is much variation in the distribution of these spines ; even in the specimens from the first two localities the margin of the carapace bears larger spines than is usual in *Lepidurus.*

Body.—Segments, 31–34 ; apodous, 3–5.

Telson.—Supra-anal plate about same size as in *L. apus,* central spines 2–7, marginals very large and sparse.

Appendages.—60–71. Endites as in *L. apus.*

Sexual dimorphism.—Normal for the genus.

Reproduction.—Bisexual.

LEPIDURUS BATESONI sp. nov.

TYPES. Holotype (♂) and two paratypes in BMNH (1911.11.8, 23542–4, Norman collection). Collected by W. Bateson.

RANGE. Russia. Probably collected at Chilik Kul in the Kazak region, where Bateson made a collection of other fresh-water entomostraca also in the Norman collection.

DESCRIPTION. Males only known. Long bodied form in general appearance (Text-fig. 2J).

Head.—Eyes and dorsal organ similar to those of *Lepidurus lynchi*. Second maxilla present and typical of the genus.

Carapace (Text-fig. 2J). Oval-round, more rounded than in *Lepidurus apus*. Carina and its terminal spine absent in all specimens seen ; position of carina demarcated only by the light streak of the dorsal blood channel of the carapace which follows the line of the carina in normal forms. Sulcus wide, rounded, with small sulcal teeth.

Body.—Segments 33, apodous 8, in all. Apodous ventral marginal spines very small and widely separated centrally, no supernumeraries.

Appendages.—49–52. Endites of first thoracic appendage (Text-fig. 10D) unique in known Notostraca ; endites 4 and 5 very short ; much more reduced than in *Lepidurus arcticus* and can scarcely have projected beyond carapace margin in life ; endite 5 of this appendage is little more developed than endite 5 of the second appendage. Endite 6 of the first appendage is fully developed and claw-like as in the subsequent appendages (in all other Notostraca the 6th endite of the first thoracic appendage is reduced to a small soft lobe at the base of the 5th endite).

Telson (Text-fig. 7B).—Supra-anal plate very similar to that of *Lepidurus lynchi*, central spines few (4), marginals few, coarse.

Sexual dimorphism.—Females unknown.

Reproduction.—Bisexual.

Note.—One of the paratypes has an abnormality of the supra-anal plate, which is reduced in size, soft, and lacks its armature.

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